

**Different Mechanisms Underlying
Adaptation to Frequent and Adaptation to Recent Conflict**

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Abstract

For successful goal-directed behavior we have to process information selectively and to continuously fine-tune selectivity of information processing. Phenomena thought to represent this fine-tuning are conflict adaptation effects in interference tasks, i.e., reduction of interference after an incompatible trial and when incompatible trials are frequent. Whereas prominent models of conflict adaptation, e.g., conflict monitoring theory, assume that both effects are based on the same neurocognitive mechanism, recent research raises doubt on that notion. In the four experiments presented in this dissertation, the hypothesis that adaptation to recent and adaptation to frequent conflict are based on different underlying mechanisms is tested further.

In *experiment 1* we used event related potentials to examine possible modulation of early visual information processing by frequent conflict. A recent study found that early visual ERP components were modulated by conflict in the preceding trial. In our study we found interference effects in N2 and P3 and modulation thereof by frequent conflict. Nevertheless, early visual ERP components were not modulated by frequent conflict, suggesting that adaptation to frequent conflict involves modulation of later cognitive processes, and in this respect is different from adaptation to recent conflict, which involves modulation of early sensory processes.

In *experiment 2* we used functional magnetic resonance imaging to examine possible modulation of early visual information processing by recent conflict. Another Stroop study showed facilitation of processing of task-relevant information by recent conflict. This result is interesting, as a related fMRI study on task-set implementation in the Stroop task has found enhancement of task-relevant information and suppression of task-irrelevant information. Conflict monitoring theory uses only one mechanism, facilitation of processing of the relevant information, for the implementation of task-sets, adaptation to recent conflict and adaptation to frequent conflict. The results of these two studies suggest different mechanisms for task-set implementation and adaptation to recent conflict. Importantly though, both studies have to be interpreted carefully.

In our study participants performed a color-word stroop task. In the same session participants performed two other tasks that were used to localize V4 and the VWFA. We observed increased activity in V4 for incompatible trials following incompatible trials while activity in the VWFA was not modulated by conflict level in the preceding trial. We conclude that adaptation to recent conflict in Stroop-like tasks seems mainly to involve enhancement of task-relevant information but not suppression of task-irrelevant information and that this mechanism

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differs from the mechanisms underlying other instances of cognitive control, such as task-set implementation and adaptation to frequent conflict.

It has been argued that anxious people, because they are more occupied by ruminations and worrying, rely more on less demanding reactive control mechanisms than on more demanding proactive control mechanisms. In *experiment 3* we tested this hypothesis in a behavioral experiment. Participants performed Stroop-like task and conflict frequency was manipulated between blocks. Participants were divided into two groups based on their scores in the state-trait anxiety inventory. We found adaptation to recent conflict in the high anxiety group only whereas both groups showed equal adaptation to frequent conflict.

In the *last experiment* we tried to replicate a recent study that found a simple dissociation between adaptation to recent and adaptation to frequent conflict. In contrast to this study though, we controlled the frequency of presentation for a subset of stimuli to rule out practice effects for specific stimulus ensembles and effects of stimulus-response contingencies. Participants performed a Stroop task and we manipulated the frequency of incompatible trials per block. A subset of incompatible and compatible trials was presented a fixed number of times and only this subset was used to test adaptation to recent and adaptation to frequent conflict effects. We found that modulation of the interference effect by recent conflict was confined to the beginning of the experiment. Nevertheless, in contrast to most studies Stroop interference in our study was higher after an incompatible trial. Most importantly, we found normal adaptation to frequent conflict, that can not explained by a reversed or absent, as in the last four blocks of the experiment, adaptation to recent conflict effect.

Considering the evidence provided by other studies and the evidence provided by the experiments presented in this dissertation it seems more and more unlikely, that adaptation to recent and adaptation to frequent conflict are based on the same underlying mechanism.

Zusammenfassung

Wenn man sich verdeutlicht, welche Menge an Informationen unseren Sinnen zu jedem Zeitpunkt zur Verfügung stehen, wird verständlich, warum wir nicht in der Lage sind, alle diese Informationen zu verarbeiten. Für erfolgreiches zielgerichtetes Verhalten ist es deshalb notwendig, Informationen selektiv zu verarbeiten. Informationen, die relevant für unsere aktuellen Ziele und Motive sind, müssen bevorzugt verarbeitet werden. Aus dieser Sicht wäre absolute Selektivität der Informationsverarbeitung optimal; da sich jedoch die Relevanz von Informationen unvorhersehbar ändern kann, scheint es plausibel, dass unser kognitives System stets auch aktuell irrelevante Informationen im Sinne einer Hintergrundüberwachung verarbeitet. Die Selektivität der Informationsverarbeitung bzw. das Ausmaß der Hintergrundüberwachung scheint dabei regelmäßig der Situation angepasst zu werden. Unsere Informationsverarbeitung bewegt sich also ständig auf einem Kontinuum zwischen den Extremen Stabilität und Flexibilität.

Im Labor werden diese Prozesse mit Interferenzaufgaben wie der Stroop-Aufgabe oder der Flanker-Aufgabe untersucht. In der Stroop-Aufgabe werden den Versuchspersonen Farbwörter in unterschiedlichen Farben präsentiert. In kompatiblen Durchgängen entspricht die Wortbedeutung der Wortfarbe (z.B. das Wort ROT in rot), in inkompatiblen Durchgängen unterscheidet sich die Wortbedeutung von der Wortfarbe (z.B. das Wort ROT in grün). Die Versuchspersonen haben die Aufgabe, die Wortfarbe zu benennen und die Wortbedeutung zu ignorieren. In der Flanker-Aufgabe wird den Versuchspersonen ein Stimulus präsentiert, der von Distraktoren flankiert wird. In kompatiblen Durchgängen sind der Zielreiz und die Distraktoren mit der gleichen Antwort assoziiert (z.B. HHH), in inkompatiblen Durchgängen mit unterschiedlichen Antworten (z.B. SHS). Die Versuchspersonen haben die Aufgabe, den zentralen Reiz zu diskriminieren und die Distraktoren zu ignorieren. Üblicherweise sind Versuchspersonen in der Lage, die aufgabenrelevante Information bevorzugt zu verarbeiten: Die Fehlerrate ist gering. An den Antwortzeiten kann man jedoch erkennen, dass auch die aufgabenirrelevante Information verarbeitet wird. Die Antwortzeiten für inkompatible Durchgänge sind länger als für kompatible Durchgänge. Interessanterweise verringert sich der Unterschied in den Antwortzeiten zwischen kompatiblen und inkompatiblen Durchgängen, wenn der vorangegangene Durchgang inkompatibel war und wenn in einem Versuchsblock viele inkompatible Durchgänge präsentiert werden. Es scheint also, dass unser kognitives System nach einem inkompatiblen Durchgang weniger durch die irrelevante Information beeinflusst wird. Auch wenn inkompatible Durchgänge häufig sind, scheint unser System die irrelevant Information stärker auszublenden. Prominente Modelle kognitiver Kontrolle interpretieren diese beiden Effekte entsprechend als Anpassung des kognitiven Systems: Unser

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kognitives System bewegt sich – weil es fast einen Fehler gemacht hat – auf dem Kontinuum stabil-flexibel in Richtung höherer Selektivität.

Interessanterweise wird diesen Modellen beiden Effekte, Anpassung an Konflikt im Vordurchgang und Anpassung an häufigen Konflikt, der gleiche neurokognitive Mechanismus zugrunde gelegt. Ergebnisse verschiedener Studien lassen Zweifel an dieser Annahme aufkommen. In einer Studie konnte die Initiierung und die Dauer der Ausführung der motorischen Antwort unterschieden werden. Während Anpassung an häufigen Konflikt sowohl in der Initiierung als auch in der Dauer der Ausführung der Antwort beobachtet wurde, zeigte sich Anpassung an Konflikt im Vordurchgang nur in der Dauer der Ausführung der Antwort. Dies spricht dafür, dass bei Anpassung an häufigen Konflikt nicht aber bei Anpassung an Konflikt im Vordurchgang die Antwortschwelle angehoben wird. In einer anderen Studie wurde Anpassung an Konflikt im Vordurchgang nur zu Beginn des Experiments gefunden, nicht aber am Ende. Anpassung an häufigen Konflikt hingegen wurde über die gesamte Zeit des Experiments beobachtet. In weiteren Studien konnte durch Verwendung des Aufgabenwechselfaradigmas gezeigt werden, dass Anpassung an Konflikt im Vordurchgang aufgabenspezifisch erfolgt, d.h. ein inkompatibler Durchgang in Aufgabe A führt zu einem geringeren Interferenzeffekt nur dann, wenn ein weiterer Durchgang mit Aufgabe A folgt. Anpassung an häufigen Konflikt hingegen führte auch zu einer Reduzierung des Interferenzeffektes in der Aufgabe, in der die Häufigkeit von inkompatiblen Durchgängen nicht manipuliert wurde.

In dieser Doktorarbeit werden vier Experimente vorgestellt, die weitere Evidenz dafür liefern, dass Anpassung an Konflikt im Vordurchgang und Anpassung an häufigen Konflikt auf unterschiedlichen neurokognitiven Mechanismen beruhen. Die Interpretation der Reduktion des Interferenzeffektes nach einem inkompatiblen Durchgang als kognitive Kontrolle ist verschiedentlich kritisiert worden, da andere sequentielle Effekte ähnliche Muster in den Antwortzeiten und Fehlerraten erzeugen können. In den hier berichteten Experimenten zur Anpassung an Konflikt im Vordurchgang wird deshalb die Stimulussequenz streng kontrolliert. Von einem Durchgang zum nächsten erfolgt stets ein kompletter Wechsel aller Stimulus-Features.

Im ersten Experiment wurde die Hypothese getestet, dass Anpassung an häufigen Konflikt frühe sensorische Informationsverarbeitungsprozesse involviert. Versuchspersonen bearbeiteten eine Eriksen-Flanker-Aufgabe während elektrische Hirnströme abgeleitet wurden. Blockweise wurde die Häufigkeit von inkompatiblen Durchgängen manipuliert. Es zeigte sich ein Flanker-Effekt in den Antwortzeiten und Fehlerraten, welche in Blöcken mit seltenem Konflikt größer war als in Blöcken mit häufigem Konflikt. In Blöcken mit seltenem Konflikt zeigte sich außerdem eine größere Amplitude der fronto-zentralen N2 und eine höhere Latenz der zentralen P3 für inkompatible Stimuli im Vergleich zu kompatiblen Stimuli. Dieser Effekt verschwand in Blöcken mit häufigem Konflikt. Auf der anderen Seite ließ sich keine Modulierung früher posteriorer ereigniskorrelierter Potentiale durch die Konflikthäufigkeit nachweisen. Anpassung an häufigen Konflikt basiert also vermutlich auf späteren Informationsverarbeitungsprozessen. Interessanterweise fand eine andere psychophysiologische Studie eine Modulierung früher posteriorer ereigniskorrelierter Potentiale durch Konflikt im Vordurchgang. Beide Studien zusammengenommen legen den Schluß nahe, dass Anpassung an Konflikt im Vordurchgang

und Anpassung an häufigen Konflikt auf unterschiedlichen neurokognitiven Mechanismen beruht.

Im zweiten Experiment wurde die Hypothese getestet, dass Anpassung an Konflikt im Vordurchgang frühe sensorische Informationsverarbeitungsprozesse, insbesondere Inhibition der Verarbeitung der aufgabenirrelevanten Information, involviert. Versuchspersonen bearbeiteten eine Stroop-Aufgabe während ihre Hirnaktivität mittels funktioneller Kernspintomographie gemessen wurde. Durch zwei unabhängige Aufgaben wurden inferotemporale Hirnareale lokalisiert, welche mit der Verarbeitung von Farben beziehungsweise Wortformen assoziiert werden. Im Vergleich zu kompatiblen Durchgängen zeigte sich in inkompatiblen Durchgängen erhöhte Aktivierung eines fronto-parietalen Netzwerks aus medialem Präfrontalkortex, ventro-lateralem Präfrontalkortex und posteriorem Parietalkortex. Zudem zeigte sich eine Modulierung der Aktivität im sensorischen Farbareal durch Konflikt im Vordurchgang aber keine Modulierung der Aktivität im sensorischen Wortareal. Anpassung an Konflikt im Vordurchgang scheint also hauptsächlich die verstärkte Verarbeitung aufgabenrelevanter sensorischer Informationen zu involvieren.

Weil ängstliche Personen mit Grübeln und Sorgen okkupiert sind, wird angenommen, dass ihnen weniger Aufmerksamkeitsressourcen zur Verfügung stehen. Sie sollten deshalb eher ressourcenschonende Strategien der Informationsverarbeitung verwenden.

Im dritten Experiment wurde die Hypothese getestet, dass ängstlichere Personen eher transiente als längerfristige Kontrollmechanismen verwenden. Die Versuchspersonen bearbeiteten eine Stroop-Aufgabe. Blockweise wurde die Häufigkeit von inkompatiblen Durchgängen manipuliert. Die Versuchspersonen wurde anhand der State-Trait-Anxiety Inventory in weniger ängstliche und ängstlichere Personen eingeteilt. Anpassung an Konflikt im Vordurchgang wurde nur für ängstlichere Versuchspersonen gefunden, während beide Gruppen Anpassung an häufigen Konflikt zeigten. Das Ergebnis spricht nicht unbedingt dafür, dass ängstlichere Personen hauptsächlich ressourcenschonende Informationsverarbeitungsstrategien verwenden. Das Ergebnis legt jedoch Unterschiede in der Anpassung an Konflikt im Vordurchgang und Anpassung an häufigen Konflikt nahe. Zudem könnte der bisher wenig beachtete Einfluß von Ängstlichkeit auf Konflikthanpassung erklären, warum in einigen Studien Anpassung an Konflikt im Vordurchgang gezeigt werden kann, in anderen hingegen nicht.

In einer interessanten Studie wurde Anpassung an Konflikt im Vordurchgang nur zu Beginn des Experiments gefunden, nicht jedoch am Ende. Anpassung an häufigen Konflikt hingegen war während des gesamten Experiments zu beobachten. Im letzten Experiment wurde versucht, die Ergebnisse dieser Studie zu replizieren. Im Gegensatz zu dieser Studie wurde im hier berichteten Experiment die Häufigkeit von bestimmten Stimuli konstant gehalten, während die restlichen Stimuli dazu verwendet wurden, die Konflikthäufigkeit blockweise zu manipulieren. Interessanterweise wurde zu Beginn des Experiments ein größerer Interferenzeffekt nach inkompatiblen Durchgängen gefunden. Nichtsdestoweniger war, wie in der erwähnten Studie, dieser Effekt am Ende des Experiments nicht mehr nachzuweisen. Anpassung an häufigen Konflikt hingegen war während des gesamten Experiments beobachtbar. Dieses Ergebnis ist schwierig zu erklären, wenn man annimmt, dass Anpassung an Konflikt im Vordurchgang und Anpassung an häufigen Konflikt auf dem gleichen neurokognitiven Mechanismus beruhen.

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Zusammengenommen legen die in dieser Doktorarbeit vorgestellten Studien den Schluß nahe, dass Anpassung an Konflikt im Vordurchgang und Anpassung an häufigen Konflikt auf unterschiedlichen Mechanismen beruht. Während Anpassung an Konflikt im Vordurchgang frühe sensorische Prozesse involviert, spielt sich Anpassung an häufigen Konflikt zu einem späteren Zeitpunkt in der Informationsverarbeitung ab.

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1

General Introduction

While our senses are able to process an enormous amount of information, we all know from our own experience that we are unable to process all information that is available in the environment at any point in time. Considering this limitation goal-directed behavior can only be successful if information processing is selective. Our cognitive system has to favor processing of information that is relevant to our current goals and motivational states over processing of information that is not. Although we are able to process information selectively, we are confronted with *failure* of selectivity at times. In these situations relevant sensory representations, irrelevant sensory representations, and response representations often share similarities with each other, which seems to make selection processes more difficult. Furthermore, based on our individual learning history associations between certain stimuli and specific responses exist. If these habits need to be overcome, errors in the sense of unwanted or unintended behaviors are more likely to occur.

Selective attention and control thereof is commonly considered to be one in a set of cognitive functions called executive functions. Other main executive functions are inhibition, working memory, and cognitive flexibility. Considering the importance of these functions for everyday life, it is no surprise to find selective attention and other executive functions as a main area of research in cognitive psychology and cognitive neuroscience (for recent reviews see Diamond, 2013; Hofmann, Schmeichel, and Baddeley, 2012).

To study selective attention in the laboratory several tasks have been developed. These tasks typically involve discrimination of a stimulus while ignoring other stimuli or discrimination of a dimension of a stimulus while ignoring other dimensions of the stimulus. In terms of

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error rates, participants' performance in these tasks is normally quite good, showing that they are able to give task-relevant information higher priority in information processing than task-irrelevant information. Nevertheless, task-irrelevant information is not filtered out completely but processed to a certain degree. This is reflected in longer response times and higher error rates for trials in which the relevant and irrelevant information do not match.

Prominent examples of such tasks are the Stroop task (Stroop, 1935; for reviews see MacLeod, 1991 and MacLeod, 2001), the Eriksen flanker task (Eriksen and Eriksen, 1974; for a review see Eriksen and Schultz, 1979), and the Simon task (Simon, Craft, and Small, 1971; for reviews see Lu and Proctor, 1995, and Simon, 1990). In the Stroop task (Stroop, 1935) color words are presented in different colors. Participants have to name the print color of the word while ignoring the word meaning. Response times are longer and error rates higher for stimuli in which print color and word meaning do not match, e.g. for the word RED presented in blue, than when color and word meaning match, e.g. for the word GREEN presented in green. In the Eriksen flanker task (Eriksen and Eriksen, 1974), participants have to indicate the identity of a letter while ignoring distractor letters which are presented on the left and right side of the target stimulus. In this task, response times are longer and error rates higher for stimulus arrays in which target and flankers are associated with different responses, e.g. for the stimulus array SHS, than for stimulus arrays in which target and flankers are associated with the same response, e.g. for the stimulus array HHH. In the Simon task (Simon, et al., 1971) participants hear a high or low pitch tone on the right or left ear. They are instructed to indicate the frequency of the tone by pressing a left or right button. In visual versions of the task, participants have to discriminate a visual stimulus that is presented on the left or right side of the screen by pressing a left or right button. Response times are longer and error rates higher for trials in which the side of presentation of the stimulus and side of the correct response differ, e.g. a high pitch tone presented on the right side calling for a left button press response, than for trials in which the stimulus is presented on the same side of the response that has to be given, e.g. a high pitch tone presented on the left side calling for a left button press response. As mentioned above, dimensional overlap has been identified as a key feature of interference tasks (Kornblum, Hasbroucq, and Osman, 1990). Following this conception interference effects mainly evolve because of cross-talk between cognitive processes if sensory features of the relevant and irrelevant stimulus (or stimulus dimensions) or sensory features and response features overlap. Dimensional overlap theory thereby offers a common taxonomy for interference tasks (see Table 1.1).

Irrespective of the task in this thesis I will use the term *compatible* when the target stimulus and distracting stimuli or target stimulus dimension and the distracting stimulus dimensions call for the same response and *incompatible* when they call for different responses. The interference effect is the difference in relevant dependent variables (e.g. response times and error rates) between these two categories of stimuli.

Table 1.1: Taxonomy of interference tasks based on dimensional overlap (adapted from Kornblum, et al., 1990).

Type	Relevant S-R Overlap	Irrelevant S-R Overlap	S-S Overlap	Example Tasks
1	no	no	no	choice reaction time task
2	yes	no	no	Fitts task
3	no	yes	no	Simon task
4	no	no	yes	Flanker task, Stroop-like tasks, cross-modal tasks
5	yes	yes	no	Hedge and Marsh task
6	yes	no	yes	
7	no	yes	yes	combined Simon and Stroop-like tasks
8	yes	yes	yes	Stroop task

As the Eriksen task (Experiment 1) and the Stroop task (Experiment 2, 3, and 4) were used in the experiments reported in this thesis a brief summary of relevant theoretical and empirical results for these tasks will be given in the following paragraphs.

1.1 Flanker Effect

The flanker effect shows the inability of our cognitive system to fully restrict visual processing to the location of the target stimulus. In the taxonomy presented in Table 1.1 the flanker task is a type 4 interference task: There is dimensional overlap between the target stimulus and the distractor stimulus. Early models of visual attention described visual attention as a spotlight moving through visual space (Posner, Snyder, and Davidson, 1980). In this metaphor only stimuli in the spotlight of attention are processed and the spotlight can be moved through the visual field to selectively process certain stimuli but not others. Interestingly, studies in which the distance of the distractors to the target in the flanker task was manipulated found increased flanker effects with flankers closer to the target (Eriksen and Eriksen, 1974). This suggests that attention either is not distributed equally within the spotlight but following a periphery to center gradient or that the size of the spotlight gets smaller during stimulus processing (Eriksen and Schultz, 1979; Eriksen and St. James, 1986). Supporting the second hypothesis using a quantile probability function it was found that accuracy gradually increased with increasing response time, i.e., accuracy was lowest—even lower than expected by chance—for fast responses and increased to higher than expected by chance levels with longer response times (Gratton, Coles, Sirevaag, and Eriksen, 1988). These results reflect the dominance of the irrelevant information of the more numerous flankers at the beginning of information processing and the gradual down-weighting of this information as information processing proceeds. Therefore visual attention is best described as a zoom-lens with a broad focus

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at stimulus onset, resulting in processing of target and flankers at this point in time, and gradual narrowing of the zoom-lens, resulting in less and less processing of the flankers with time. Flankers get excluded from information processing earlier the greater the distance between flankers and target and hence the flanker effect gets smaller with increasing distance between flankers and target. Another important finding was that muscle activity associated with the incorrect response could be measured in incompatible trials (Coles, Gratton, Bashore, Eriksen, and Donchin, 1985). In this study participants had to perform a flanker task with two stimuli and two responses. They had to indicate the identity of the central letter (H or S) by squeezing a dynamometer with their right or left hand. This response device allowed to register sub-threshold activation of both responses. Furthermore, electromyographic activity of the flexor muscles of the forearm was measured. This allowed to register activation of muscles involved in giving a response even before grip force increased. On a number of trials and more often for incompatible trials concurrent activation of both response channels was found in electromyographic activity and sub-threshold squeezing. This result suggests that information is not processed in a stage-like manner (Sternberg, 1969) but continuously (Eriksen and Schultz, 1979). Sensory stimulus processing can influence response preparation even before stimulus processing has ended. Still, the notion of information processing stages seems still useful—if only to help us to grossly structure our thinking of information processing.

From a reverse engineering point of view any system able to perform the flanker task has to be able to represent the task rules (e.g. stimulus-response mapping), to encode the identity and location of the stimuli and to translate these sensory representations into the appropriate motor responses. A parallel distributed processing model has been developed implementing these processes (Cohen, Servan-Schreiber, and McClelland, 1992). This model is comprised of a network built from singular information processing units that—from a mathematical point of view—mimic neurons. The network hierarchically organized in layers. Each unit gets input from units in downstream layers. All input signals that a unit receives are integrated using a mathematical function (e.g. a sigmoid function) and the resulting value is then given as input into connected units in upstream layers. Furthermore, units processing similar information are grouped into modules and units in one module are connected with each other by inhibitory connections (simulating cross-talk). On the other hand, connections between units in different modules are strictly excitatory.

As illustration a model for an Eriksen flanker task with two stimuli (H and S) and two responses (H and S) is presented in Figure 1.1 on page 5. At the sensory level there is one module containing six units each representing a specific stimulus at a specific location, e.g. H_1 , the letter H in the left position of the stimulus array. Stimulus information gets fed into the system by activating the respective sensory units. At the response level there is one module containing two units, one representing the response H and the other representing the response S. All input units representing one specific letter have excitatory connections to the corresponding response unit. If the activity of one of the response units exceeds a certain threshold, the corresponding response gets executed. The response time of this system is the number of cycles it needs for one response unit to reach the response threshold. To enable the system to respond

to stimuli in any of the three positions, there is an attention module which contains units for each of the three positions. These units have excitatory connections to corresponding units in the input module, so that the sensory unit processing the stimulus at the corresponding position gets an additional excitatory input. This results in a processing advantage for stimuli at the attended position. Variability is introduced by adding Gaussian noise to the input of all units. One trial in this simulation comprises the following: The task instructions define the central position in the stimulus array as the relevant position. Therefore, the central unit in the attention module is active. This activation spreads to the input units H_c and S_c . If the stimulus array HHH is presented, the units H_l , H_c , and H_r in the input module get activated. Activation spread from the input module to the response module. The H unit in the response module gets activated by connections with H_l , H_c , and H_r and hence the response threshold is reached early. If the stimulus array SHS is presented, the S_l and S_r units and the H_c unit in the input module get activated. The activation from the S_l and S_r units in the input module spread to the S unit in the response module. The activation from the H_c unit in the input module spread to the H unit in the response module. Therefore both units in the response module get activated and—because there are inhibitory connections between units that reside in the same module—reaching the response threshold later. Activation of the H unit in the response module can win against activation of the S unit in the response module because the H_c unit in the input module gets the additional excitation by the attentional unit. As activation levels of units get updated every simulation cycle, information flows continuously through the system.

This model is able to simulate response time and error rate patterns found in the literature. For instance, it can successfully simulate the data of Gratton, et al., (1988) with below chance accuracy for fast responses and increasing accuracy with increasing response times. The model further makes clear that cognitive interference can happen at different stages of information processing.

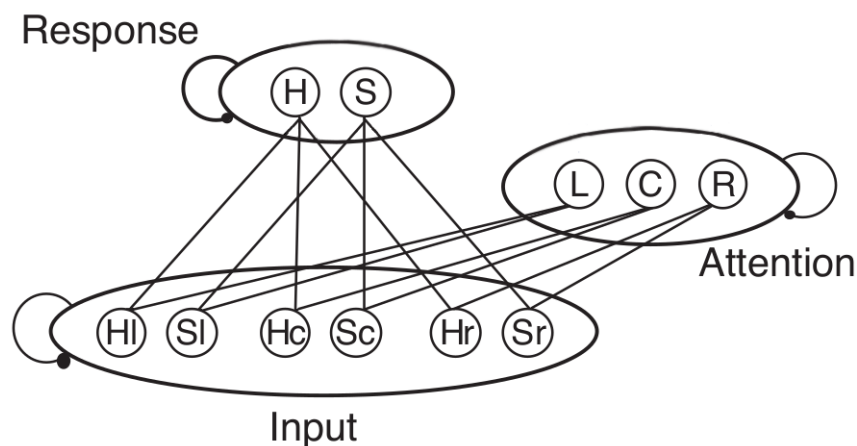


Figure 1.1: PDP-model of the Eriksen flanker task (adapted from Botvinick, Cohen, and Carter, 2004).

It has to be noted that although in this model the top-down influence on information processing is implemented in a specific way (facilitation of sensory processing of stimuli at the central position; Cohen, et al., 1992, p. 256), the model is under-determined with respect to the exact mechanisms of task-set related top-down control. In other words, empirical results could be simulated equally well with models using different mechanisms. Concerning task-set-related control in the flanker task, the influence of the target stimulus on response selection could be increased by facilitation of processing of stimuli in the central position of the stimulus array, by suppression of processing of stimuli in the lateral positions of the stimulus array, by facilitation and suppression, by strengthening the coupling between sensory units processing stimuli at the central position and the corresponding responses or by weakening the coupling between sensory units processing stimuli at the lateral position and the corresponding responses (i.e., altering stimulus-response translation), or by increasing the response threshold. While the first three mechanisms would be classified as early selection, the latter two mechanisms would be classified as late selection.

1.2 Stroop Effect

That the Stroop effect is not caused by a general inability to process one dimension of a stimulus with absolute selectivity is shown by the asymmetry of the Stroop effect: Normally, word meaning interferes with naming the color but the color does not interfere with reading the word. In contrast to the classical Stroop task in which participants have to say aloud the color, in the experiments presented in this thesis participants had to indicate the color by button press. Such tasks are preferably called Stroop-like tasks, and in the dimensional overlap taxonomy are type 4 tasks. The earliest theories on the causes of Stroop interference highlighted that word reading in our culture is more practiced than naming a color (e.g. Stroop, 1935). These models further proposed that interference results mainly from differences in processing speed. Because word information is processed faster, it wins an imaginary *horse race*, reaching the response stage of information processing first and thereby gaining exclusive access to response preparation. For a compatible stimulus this leads to a fast correct response. For an incompatible stimulus the wrong response code gets activated, leading to an error if executed or to a slow correct response if overcome by additional control processes. These models also provide a plausible explanation for the asymmetry of the interference effect. Because word information always gets exclusive access to the response stage before color information, color naming cannot interfere with word reading. Nevertheless, if processing speed were an important factor of the interference effect we should be able to eliminate and even reverse the interference effect by giving the relevant but more slowly processed stimulus dimension a head start. A study presenting the color information up to 400 ms before the word information found that this manipulation does not significantly alter the interference effect (Glaser and Glaser, 1982). Also making processing of the irrelevant information harder and hence slowing down its processing, should eliminate the interference effect. Here again empirical evidence speaks against processing speed: If the word is presented upside down,

reading the word is slowed down substantially but Stroop interference is basically unaltered (Dunbar and MacLeod, 1984). There are also situations in which color naming can interfere with word reading, for instance when participants have to switch between color naming and word reading between blocks (Allport, Styles, and Hsieh, 1994; Allport and Wylie, 1999). That processing speed is an important factor of the interference effect is therefore unlikely. Nevertheless, that word reading practice might be relevant was a significant observation. The importance of practice has been confirmed by studies in which participants were trained on arbitrary naming tasks (MacLeod and Dunbar, 1988). The direction and the size of interference effects could be predicted on the level of practice for each task. Current theories note that practice leads to automaticity in information processing. Automatic processes have been defined as being effortless, unconscious, and involuntary (e.g. Posner, 1978). It turned out that it is hard to find a process that fulfills all of these criteria. Furthermore, while a well practiced task interferes with a less practiced task, this less practiced task can interfere with an even lesser practiced task (MacLeod and Dunbar, 1988). Therefore, automaticity of information processing should be seen as a dimension with the extremes of automatic and controlled processing and not as a strict dichotomy.

Taking again the perspective of an engineer, for successful task performance in the Stroop task the cognitive system has to encode the color and meaning of the word, to prepare the motor response according to the task rules and finally to execute that response. It also have to have a mechanism of switching between naming the color and naming the word. Similar to the model described above for the Eriksen flanker task, a neural network model of the Stroop task has been developed (Cohen and Huston, 1994; Cohen, Dunbar, and McClelland, 1990). As illustration a simplified model for a Stroop task with three stimuli and two responses is depicted in Figure 1.2 on page 9. At the sensory level there are two modules, one representing the color and another representing the word. Each sensory module is composed of three units. In the word module there is one unit for the word RED, one for the word GREEN, and one for a neutral word. In the color module there is one unit for the color red, one for the color green, and one for a neutral color. Neutral in this context means this stimulus feature is not associated with any response in this task. The neutral condition allows to further distinguish the disadvantage of processing the task-irrelevant information (interference, the differences in response times for incompatible and neutral trials) and the advantage of processing the task-irrelevant information (facilitation, as the difference in response times for neutral and compatible trials). Each of the non-neutral units is connected to the corresponding unit in the response module. If the activity of one of the units in the response module exceeds a certain activation threshold, the corresponding response program gets executed. As an example: If the word RED is presented in red, the RED unit in the word meaning module and the red unit in the word color module get activated. Activation of these units spreads to the corresponding red unit in the response module. Therefore the red unit in the response module gets activated by two pathways and hence reaching the response threshold early. If, on the other hand, the word RED is presented in green, the RED unit in the word meaning module and the green unit in the word color module get activated. Activation of the unit in

the word meaning module spreads to the corresponding red unit in the response module and activation of the unit in the color module spreads to the corresponding green unit in the response module. Therefore both units in the response module get activated and—because there are inhibitory connections between units that reside in the same module—reaching the response threshold later. How strong a sensory unit activates a response unit depend on the learning history of the system. The model is trained by means of back-propagation or a similar algorithm. Connections between units that lead to a correct response of the network get stronger, i.e. their connection weights are increased, and thereby leading to stronger coupling of the connected units. The larger amount of practice with word reading is implemented by training the network model longer for producing the correct response for word information and word information therefore leads to stronger activation of corresponding response units than color information. That the system can still respond to the color information is realized by a task-demand module, that give excitatory input to units in the color module.

In an earlier version of the model there was an intermediate level of units between the sensory level and the response level (Cohen, et al., 1990). Computationally, this level has been included into the sensory level in later models. From a conceptual point of view this step was unfortunate. Although with respect to the simulation the difference is negligible, the intermediate level could be thought of as holding a more abstract representation of the information represented in the sensory units. While the task demand units influence units at the intermediate level in the earlier model, they influence units at the sensory level in the later models. Therefore the later models imply a direct modulation of sensory representations, an implication not found in the earlier model.

In any case, this model is able to simulate response time and error rate patterns from the extensive empirical literature on experimental manipulations in the Stroop task. For instance, in simulations with this model word reading is faster than color naming, word reading is not affected by the color of the word but word meaning interferes with color naming, and there is greater interference for incompatible stimuli than facilitation for compatible stimuli. As for the model of the Eriksen flanker task it has to be noted that this model is under-determined with respect to the exact mechanisms of top-down control, and for the early version of the model the authors state that they "do not know whether attention is primarily excitatory (sensitizing task-appropriate units), inhibitory (desensitizing inappropriate units), or (as [they] suspect) some of both" (Cohen, et al., 1990, p. 338). In the later model connections between modules are strictly excitatory (Cohen and Huston, 1994 p. 463). Whether inhibition is one of the mechanisms of cognitive control is currently still highly debated. Some authors argue that top-down inhibition is biologically implausible, as inhibitory connections in the human brain are strictly local (Herd, Banich, and O'Reilly, 2006). However, while inhibition plays a key role for information processing in small neural networks, GABAergic (i.e., inhibitory) projection neurons have been found in the brain as well (originating in the septum region, the hippocampus and the neocortex; Tamamaki and Tomioka, 2010). Additionally, glutamatergic (i.e., excitatory) projection neurons could result in inhibition of a brain area when synapsing on local inhibitory neurons. Given these two arguments, there seem to be no biological reasons

to exclude long-range inhibition as a mechanism a-priori. Furthermore, it is important to note that in other psychological models successful task performance in the Stroop task is often thought to result solely from suppression of task-irrelevant information. For instance, the greater Stroop effect in older adults (e.g., Logan, 1980; West and Alain, 2000; Langenecker, Nielson, and Rao, 2004) and in patients with schizophrenia (e.g., Henik et al., 2002; Henik and Salo, 2004) is proposed to result from a decline in the ability to inhibit processing of irrelevant sensory input (e.g., Cohn, Dustman, and Bradford, 1984; Dulaney and Rogers, 1994). Similarly, deficits in inhibitory functions was proposed to underlie working memory impairment in the elderly (Gazzaley, Cooney, Rissman, D'Esposito, 2005). Importantly, empirical results could successfully be simulated with models using different mechanisms. Concerning task-set-related control in the Stroop task, the influence of the color of the stimulus on response selection could be increased by facilitation of processing of color information, by suppression of processing of word information, by facilitation and suppression, by strengthening the coupling between sensory color processing and the corresponding responses or by weakening the coupling between sensory word processing and the corresponding responses (i.e., altering stimulus-response translation), or by increasing the response threshold. Here again, the first three mechanisms would be classified as early selection, the latter two mechanisms would be classified as late selection.

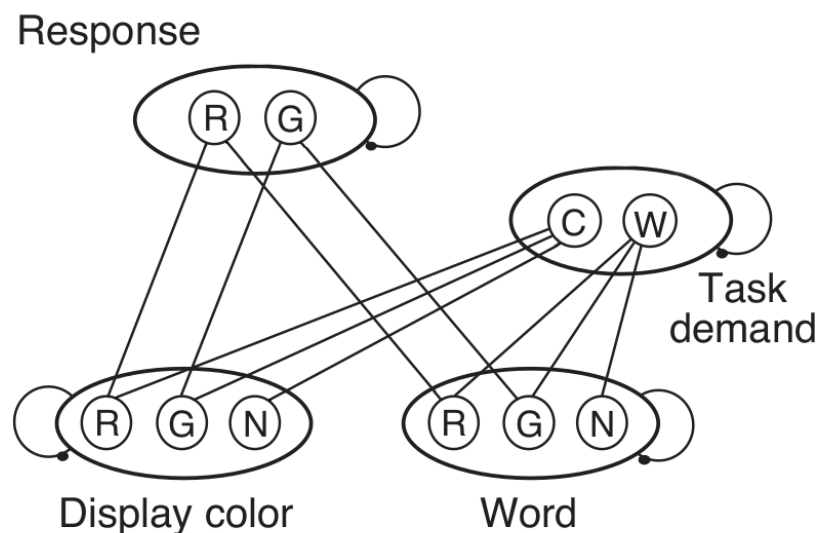


Figure 1.2: PDP-model of the Stroop task (adapted from Botvinick et al., 2004).

1.3 Conflict Adaptation

While absolute selectivity is often seen as ideal and less than absolute selectivity treated as *failure* of attention, less than absolute selectivity might have advantages too. Monitoring the environment to a certain degree might have well supported survival, for instance when a hungry carnivore came around the corner while our ancestors were collecting mushrooms.

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While we do not encounter such situations very often nowadays, our environment still can be dangerous. For instance, you might be hit by a car while crossing a street when you were too focused on your smart-phone screen and not noticing the car approaching. Variants of this sabbertooth-tiger example can be found often in the literature, unfortunately these examples have some shortcomings (see below).

In everyday life and during performance of tasks used in laboratory research our cognitive system moves along a continuum from more to less selective information processing (Durstewitz and Seamans, 2008; Diamond, 2013) and selectivity of information processing is set in accordance with the situation or task context. This fine-tuning can occur on a short temporal scale of a couple of milliseconds to seconds (Gratton, Coles, and Donchin, 1992; Kerns et al., 2004). For instance, the flanker effect is reduced when in the directly preceding trial an incompatible rather than a compatible stimulus was presented (e.g., Gratton, et al., 1992; Ullsperger, Bylsma, and Botvinick, 2005). A similar reduction in interference has been found when the frequency of incompatible stimuli increases (Gratton, et al., 1992). Both, adaptation to recent conflict and adaptation to frequent conflict, have also been found in other paradigms, such as Stroop-like tasks (e.g., Kerns et al., 2004; Logan and Zbrodoff, 1979) or the Simon task (Hommel, 1994; Stürmer, Leuthold, Soetens, Schröter, and Sommer, 2002) suggesting a general underlying mechanism. Similar behavioral effects have also been shown for processing of errors. In interference tasks reduced interference has been found for trials following error trials (King, Korb, von Cramon, and Ullsperger, 2010). Current models of cognitive control account for such modulations by assuming that processing becomes more selective regarding the relevant stimulus or stimulus dimension due to conflict between competing responses. Furthermore, responses for trials following an error are slower (but not necessarily more accurate; see Rabbitt and Rodgers, 1977), probably reflecting increased response caution (Dutilh et al., 2012). Readjusting the response threshold might also be relevant for adaptation to recent and frequent conflict (Gratton, et al., 1992).

In the everyday example given earlier, you might disengage from your smart-phone activities for a period of time after having almost been run over by a car. You might also allow yourself to be more occupied by your smart-phone when you walk a neighborhood without much traffic but you might monitor the environment to a higher degree if you walk in a busy neighborhood, where the expected likelihood of being hit by a car is higher. While certainly the processes examined in the laboratory tasks described above play a role for the behavior in this everyday example, the effects we see in the laboratory tasks are not fully captured by the example. In the laboratory tasks task-irrelevant information gets filtered out better after cognitive conflict, while in the everyday example both the smart-phone and the traffic are more or less relevant. Due to conflict the previously less task-relevant information (traffic) gets now processed with higher priority. A better everyday example therefore might be the situation of someone who wants to reduce his or her body weight. The desire to eat sweets, cake or otherwise unhealthy food will evolve despite the long-term goal of weight reduction. Furthermore, these desires are triggered by the view and smell of such food items. This opens the possibility that attentional modulation of sensory processes might be one mechanism used by our cognitive system

to prevent unwanted behaviors. One might imagine that after having experienced such a desire, individuals could be better able to focus on the long-term goal and be better able not to be influenced by the desired food. One might further imagine, that when these individuals visit a place where unhealthy food has to be expected, they might be *prepared* and inhibit processing of sensory (view and smell) information related to the desired food items. Also in this example the processes examined in the laboratory tasks described above certainly play a role. This is also underlined by a recent study that found that individuals high in inhibitory control (operationalized as the size of the Stroop effect) tried more often to withstand food desires, did consume less unhealthy but desired food and lost more weight than individuals low in inhibitory control, although both groups showed the same frequency and strength of desires (Hofmann, Adriaanse, Vohs, and Baumeister, 2014). Again one might argue that this example does not fully capture the effects found in the laboratory tasks, as conflict in this example arises from contradicting motives. Most importantly, these instances show a phenomenon frustrating for students and teachers of cognitive psychology alike, namely that finding good everyday examples for laboratory effects often is difficult. The reason is that even simple everyday behavior is quite complex whereas the main goal of laboratory research is high internal validity, which accomplished mainly by reduction of complexity. Ecological validity is only secondary. A more complex theory uniting the many theories on behavioral effects in the laboratory seems highly desirable, but except for single attempts, such as ACT-R (Anderson et al., 2004), the field of cognitive psychology is still highly fragmented.

1.3.1 Validity of Conflict Adaptation Effects

It is important to note that the interpretation of a reduced interference effect after incompatible trials as conflict adaptation has been challenged. As this effect is sequential in nature, other sequential effects have to be ruled out as alternative explanations of this pattern in response times and error rates. Negative priming is a well known effect (see Fox 1995; May, Kane, and Hasher, 1995) and in the Stroop task longer response times have been found when the word of one trial becomes the color in the next trial (Dalrymple-Alford and Budayr, 1966). Similarly, if participants have to give the same response as in the preceding trial, response times are faster (response priming, Bertelson, 1961). Such effects are not confined to the directly preceding trial but can be shown to exist for the last five trials (Remington, 1969). In general, to control for these sequential effects seems reasonable, although the interaction of these effects and their influence of response time patterns with respect to compatibility level in the preceding trial remains unclear. In the conflict adaptation effect incompatible trials following incompatible trials are normally faster than incompatible trials following compatible trials. Furthermore, compatible trials following compatible trials are faster than compatible trials following incompatible trials. In other words, there seems to be an advantage for trials in which the compatibility level gets repeated. Of interest, for the Simon task it has been argued that the pattern of reduced interference in response times (and error rates) after an incompatible trial can be explained by the sequence of specific stimulus-response features without the need for assuming cognitive control (event file theory, Hommel, 1998; Hommel,

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Proctor, and Vu, 2004). Inherently, in the Simon task there are only two stimuli and responses. With this setup an incompatible trial following an incompatible trial either the response and location of the stimulus gets repeated or both change. If, on the other hand, an incompatible trial follows a compatible trial, either the response changes or the location of stimulus presentation changes but never both. Similarly, a compatible trial following a compatible trial consists either of repetition or change of both stimulus and location. On the other hand, if a compatible trial follows an incompatible trial, either the stimulus or the location gets repeated but never both. Partial repetition of stimulus-response features have been associated with a response time cost (Hommel, 1998). Our cognitive system is thought to continuously encode stimulus-response features. With partial repetition the repeated feature activates the previously associated feature, causing interference and hence prolonged response times and a higher error rate. It is therefore possible that reductions of interference effects after a conflict trial reflect such processing disadvantages rather than an adjustment of selectivity (Hommel, et al., 2004).

A similar argument has been made for the Eriksen task (Mayr, Awh, and Laurey, 2003). It is argued that because in half of all incompatible to incompatible trial transitions target and flankers get repeated, there is a response time benefit for these transitions. If complete repetitions were excluded from the analysis, the adaptation pattern disappeared.

However, adaptation to recent conflict has been found even after excluding target and distractor repetitions from the analysis (Kerns et al., 2004, Ullsperger, et al., 2005, Purmann, Badde, and Wendt, 2009). Hence, behavioral adaptations after conflict situations seem to occur, although to a smaller extent than previously thought and only under certain conditions. Nevertheless, overall these results point out the necessity to control for stimulus-response sequence effects to infer cognitive control (see Duthoo, Abrahamse, Braem, Boehler, and Notebaert, 2014 for a review). Unfortunately, most studies in the field did not or at least did not sufficiently control for non-attentional accounts of conflict adaptation effects, rendering interpretation of the results of these studies difficult. Non-attentional sequential effects in interference task can be controlled post hoc, by excluding problematic stimulus sequences from the analysis (Purmann, et al., 2009), or in advance, by using pseudo-random stimulus sequences that do not contain problematic stimulus sequences (see Chapter 3, 4, and 5). Both strategies benefit from or even require a greater number of stimuli and responses. When using the first strategy there is a substantial loss of data, leading to longer experiments, increased number of participants, and/or fewer factors examined per experiment. On the other hand, when using non-random stimulus sequences our cognitive system might form expectations. From my experience a significant number of participants is aware of constraints in stimulus-sequences. Some participants report that they noticed that the color in one trial never was the color in the following trial in an informal interview after the experiment, which is part of the debriefing. The consequences of the awareness of constraints in the stimulus sequences have not been investigated so far, but it seems plausible to assume that the impact might be higher the smaller the number of stimuli and responses is.

The interpretation of reduced interference effects under conditions of a higher frequency of incompatible trials as cognitive control adjustments is similarly difficult. Often it is assumed that the flankers are irrelevant to the task and hence the flanker effect demonstrates failure of selective attention. Nevertheless, in the case of an Eriksen task with two stimuli (H and S) and two responses (left and right button press) presenting incompatible stimuli more or less often than compatible stimuli (adaptation to frequent conflict) results in a correlation between flankers and responses. In task blocks with a high frequency of incompatible trials the stimulus array HSH occurs more often than the array HHH and hence when H occurs as flanker a right button press is the correct response in most trials. Likewise, in these blocks SHS occurs more often than SSS and hence when S occurs as flanker a left button press is the correct response in most trials. In other words, under conditions of an unequal number of presentations of incompatible and compatible trials, the irrelevant information actually contains relevant information (Mordkoff, 1996). This flanker-response contingency leads to faster responses to incompatible stimuli when incompatible stimuli are more frequent. Hence a reduced interference effect under these conditions might (at least partially) be explained by this contingency effect. This reasoning is also important for adaptation to recent conflict when more than two stimuli and responses are used. If the frequency of compatible and incompatible stimuli is held constant and both categories of stimuli are presented the same number of times, any specific compatible stimulus is presented more often than any specific incompatible stimulus. Relevant confounds for adaptation to recent and frequent conflict are not easily controlled, as either a high number of trials has to be excluded from analysis or stimulus sequences with complex constraints have to be created.

1.3.2 Same or Different Underlying Mechanisms?

To be able to cope with adaptation to recent and adaptation to frequent conflict the neural network models introduced above have been adapted (Botvinick, Braver, Barch, Carter, and Cohen, 2001). The adapted model (see Figure 1.3 on page 14) accounts for response conflict as concurrent activation of divergent response units, measured as Hopfield energy, and cognitive control as "preactivation" of units in the color module. In this model conflict in one trial influences the amount of cognitive control occurring in the following trial, as expressed in the following equation:

$$C(n+1) = \lambda C(n) + (1 - \lambda)(\alpha(E(n) + \beta))$$

Cognitive control in the following trial $C(n+1)$ is a function of the amount of control in the current trial $C(n)$, and the level of conflict in the current trial $E(n)$, such that control in the following trial is increased after a conflict trial and decreased after a non-conflict trial. The level of conflict in the current trial, on the other hand, depends on the amount of control in the current trial in that the higher the control in a trial, the smaller the response conflict. The parameters α and β are scaling parameters, and λ weights the influence of conflict in the preceding trial. From this equation it follows that with each incompatible trial, cognitive

control is increased (adaptation to recent conflict). When there is a series of incompatible trials this adaptation accumulates until a maximum amount is finally reached. Cognitive control is therefore higher on average when incompatible trials are frequent, and hence the interference effect is smaller under these circumstances (adaptation to frequent conflict). In this model, therefore, both adaptation to recent conflict and adaptation to frequent conflict are based on the same mechanism. It is further important to note that increased selectivity in these instances is realized by the same mechanism that is used to implement the task-set in these tasks, or in other words, recent and frequent conflict leads to strengthening or refreshing of the task-set.

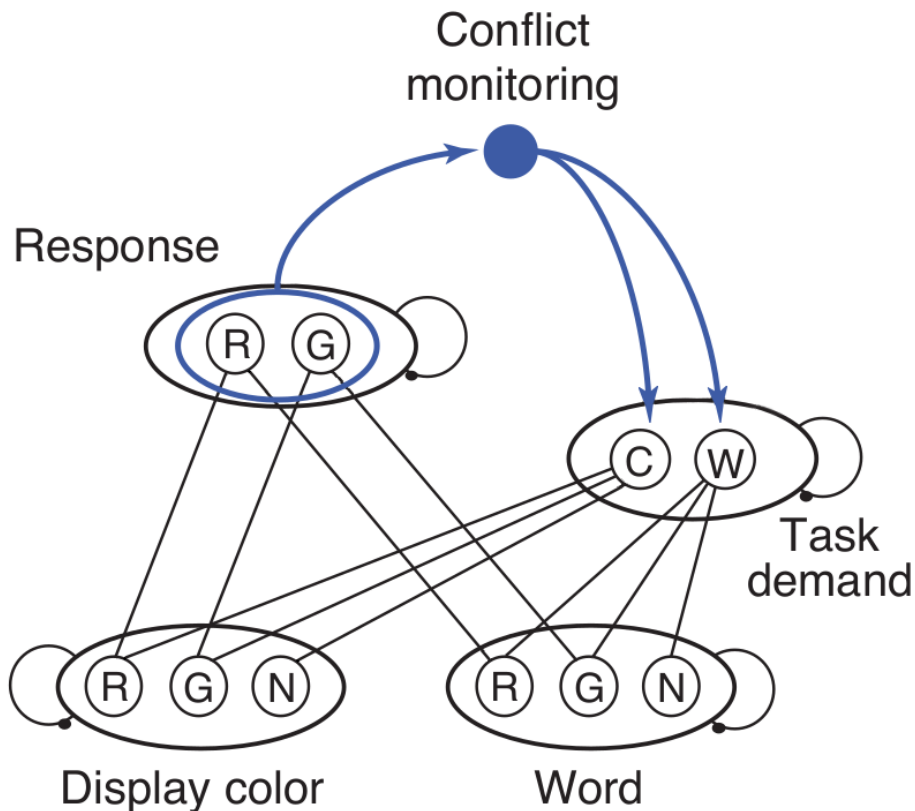


Figure 1.3: PDP-model of the Stroop task with Conflict Adaptation (adapted from Botvinick et al., 2004).

An alternative model (Gratton et al., 1992) postulates that responses can be given based on information in an early parallel or a late focused phase of information processing. During the early phase task-relevant and task-irrelevant information is processed. During the late phase our cognitive system is able to separate task-relevant and task-irrelevant information and to decrease the influence of task-irrelevant information on response preparation (by undefined mechanisms). A response given during the early phase will lead to a fast correct response for compatible stimuli and an error for incompatible stimuli. A response given during the

late phase, on the other hand, will lead to a slow but correct response for compatible and incompatible stimuli. The authors argue that when participants expect an incompatible stimulus they strategically use information during the late phase to optimize task performance. This expectation can arise because of conflict in the preceding trial, frequent conflict, or from being cued on the likely conflict level of the upcoming stimulus. In this model—despite the differences to conflict monitoring theory—adaptation to recent and adaptation to frequent conflict are based on the same underlying mechanism as well.

Recently, a number of empirical results have raised doubts on the notion of a one-fits-all mechanism. In a study using the flanker task the overall frequency of compatible and incompatible stimuli was varied between two groups of participants and a dissociation between both adaptation effects was found (Purmann, et al., 2009). In this study response times were decomposed into movement initiation times and movement execution times. Whereas adaptation to frequent conflict was evident in movement initiation and execution times, adaptation to recent conflict was confined to movement execution times. Another study (Mayr and Awh, 2009) used a Stroop task and found adaptation to recent conflict in the first two blocks of the experiment only. In contrast, adaptation to frequent conflict was found over the whole course of the experiment. Another study used two different interference tasks to test if adaptation effects transfer from one task to the other (Fernandez-Duque and Knight, 2008) and found both – adaptation to recent and adaptation to frequent conflict – to be task-specific. Nevertheless, adaptation to recent conflict in this study could be fully explained by episodic memory retrieval effect (see below) while adaptation to frequent conflict was still present after controlling for these effects. Another series of studies examined the task specificity of conflict adaptation processes. In one study trials of a spatial Stroop task and a Simon task were presented in random order (Funes, Lupiáñez, and Humphreys, 2010). They found only adaptation to frequent conflict to be task-general. Adaptation to recent conflict did not generalize to the other task. In a follow-up study one group of subjects worked on two blocks of trials of the Simon task with a 75/25 ratio of compatible trials to incompatible trials, while another group worked on two blocks of trials of the Simon task with 25/75 ratio of compatible trials to incompatible trials (Torres-Quesada, Funes, and Lupiáñez, 2013). In the following blocks trials of a flanker task were intermixed within trials of the Simon task. It was found that adaptation to recent conflict was task-specific, but adaptation to frequent conflict generalized to the other task. Furthermore, adaptation to frequent conflict was found to be a sustained effect, as it could still be observed in the first two post-training blocks with a 50/50 ratio of compatible to incompatible trials.

The neural network models presented above are supposed not only to model behavior but to do so in a biologically plausible way. This is another important aspect of these models, because it establishes constraints in modeling and allows to test the models through cognitive neuroscience methods such as event-related brain potentials (ERPs) or functional magnetic resonance imaging (fMRI). As stated above, in most cases, the behavioral effects attributable to cognitive control can be accounted for equally well by different mechanisms (MacLeod, Dodd, Sheard, Wilson, and Bibi, 2003). Therefore, making use of cognitive neuroscience

methods might be a fruitful—although not the only—strategy to pin down the exact mechanisms of cognitive control.

From a system level perspective certain brain areas have been associated with different modules in the model. For instance the anterior cingulate cortex (ACC) has been linked to the conflict monitoring module in the model and the dorso-lateral prefrontal cortex (DLPFC) has been linked to the task demand module (Botvinick, et al., 2001). Activity in certain brain areas and the amplitude and latency of certain event related brain potentials can be used as indicators for activation of certain parts/functions/modules in cognitive models. For instance a recent study showed that adaptation to recent conflict is associated with modulation of early posterior event related potentials (Scerif, Worden, Davidson, Seiger, and Casey, 2006). In this study, participants performed an arrow flanker task. Trials that were preceded by incompatible trials were compared to trials preceded by compatible trials. They found an increased amplitude of the posterior P1 for incompatible trials following incompatible trials and concluded that adaptation to recent conflict involves modulation of early visual information processing. If adaptation to recent conflict and adaptation to frequent conflict were based on the same neurocognitive mechanism, one should find modulation of early event related potentials (ERPs) for adaptation to frequent conflict. In the first experiment we used event-related brain potentials to examine modulation of early posterior components under conditions of varying frequency of incompatible trials in a flanker task. We found that for incompatible trials the amplitude of the frontal N2 was increased (flanker effect) and that this effect was reduced when incompatible trials were more frequent (adaptation to frequent conflict). We further found similar effects for the P3. Most importantly, although we found the amplitude of the posterior N1 and P1 increased for incompatible trials, this effect was not modulated conflict frequency. Additionally, a search task that was presented on some trials instead of a flanker trial did not show an effect of narrowed spatial attention. We interpreted our results in the following way: The difference in the amplitude of the N2 and P3 results from higher response conflict for incompatible trials and the modulation of this effect by conflict frequency indicates that response conflict is reduced by attentional mechanisms when conflict is frequent. Nevertheless, these attentional mechanisms do not involve modulation of early sensory information processing but later—possible response related—processes. Given that adaptation to recent conflict has been shown to involve modulation of early sensory information processing, our results further support the idea, that adaptation to recent and adaptation to frequent conflict are based on different underlying mechanisms.

Event related potentials have the advantage of high temporal resolution, but suffer from low spatial resolution. On the other hand, functional magnetic resonance imaging has high spatial resolution but low temporary resolution. Therefore, modulation of early posterior ERPs show that adaptation to recent conflict occurs early in information processing, the exact anatomical location and nature of this modulation has to remain unclear. Whether adaptation to recent conflict is mediated by enhancement of processing of task-relevant information, suppression of processing of task-irrelevant information, or by both has been examined explicitly in an fMRI study (Egner and Hirsch, 2005). In this study, participants saw faces of politicians

and actors. Overlaid on the faces the names of politicians and actors were presented. In some blocks participants had to indicate if the face belongs to a politician or an actor, in other blocks they had to indicate if the name belongs to a politician or an actor. Activation changes in the fusiform face area depended on the compatibility level of the preceding trial was examined. Increased activation of this area was found after an incompatible trial, but only when faces were the task-relevant stimulus. No modulation by compatibility level of the preceding trial was found when the names were the task-relevant stimulus. The authors suggest that adaptation to recent conflict involves enhancement of processing of task-relevant information but not inhibition of processing of task-irrelevant information. This result is interesting, as a related fMRI study on task-set implementation in the Stroop task has found enhancement of task-relevant information and suppression of task-irrelevant information (Polk, Drake, Jonides, Smith, and Smith, 2008). In this study participants had to perform blocks of a Stroop task, with all stimuli being incompatible in some blocks and neutral in other blocks. For incompatible compared to neutral Stroop blocks they found increased activity in V4, an inferotemporal brain area related to color processing (Bartels and Zeki, 2000), and decreased activity in the VWFA, an inferotemporal brain area related to word processing (Cohen et al., 2000), and followed that both enhancement of processing of color information and suppression of processing of word information is part of task-set implementation. As stated earlier, the connectionist model uses only one mechanism—enhancement of processing of the relevant information—for task-set implementation, adaptation to recent conflict and adaptation to frequent conflict. The results of these two studies suggest different mechanisms for task-set implementation and adaptation to recent conflict.

Importantly though, both studies have to be interpreted carefully. The first study uses a face-word Stroop task which—in contrast to the color-word Stroop task—uses non-integrated stimuli. Interference effects in Stroop-like tasks with non-integrated stimuli have been shown to be smaller (MacLeod, 1991), suggesting differences in the underlying mechanisms. If effects found in the face-word Stroop task generalizes to the color-word Stroop task (and vice versa) is currently not known. Furthermore, in the experimental design they used, participants had to switch between face discrimination and word discrimination in a block-wise fashion. This manipulation was necessary to be able to examine activity in the FFA under two conditions, when faces were task-relevant and task-irrelevant, respectively. It is known that switching between two task-sets in a block-wise fashion can lead to carry-over effects from one block to another (Allport et al., 1994; Allport and Wylie, 1999; Monsell, 2003). The presence of task-set inertia is reflected in the observation that participants in this study showed interference effects under both task-sets, while normally Stroop interference is asymmetric. Nevertheless, how task-set inertia effects interact with conflict adaptation effects is currently not well understood. In the second study transient and sustained effects cannot be separated because of the use of a block design. The observed facilitation and inhibition effects can therefore reflect task-set implementation, adaptation to recent conflict, and/or adaptation to frequent conflict.

We conducted an fMRI experiment (see Chapter 3) to further clarify the neural mechanisms underlying adaptation to recent conflict. Participants performed a color-word Stroop task. In

the same session participants also performed two other tasks that were used to localize V4 and the VWFA. During the Stroop task we observed increased activity in V4 for incompatible trials following incompatible trials whereas activity in the VWFA was not modulated by conflict level in the preceding trial. We thereby replicated the results from the face-word Stroop task. We conclude that adaptation to recent conflict in Stroop-like tasks (color-word Stroop task, face-word Stroop task) seems to mainly involve enhancement of task-relevant information but not suppression of task-irrelevant information and that this mechanism differs from the mechanisms underlying other instances of cognitive control, such as task-set implementation and adaptation to frequent conflict. Furthermore, as modulation of early visual information processing was restricted to incompatible trials following incompatible trials—and this is true for the three studies (Egner and Hirsch, 2005, Scerif, et al., 2006, Purmann and Pollmann, 2015)—the idea of the connectionist model presented above that adaptation to recent conflict is based on facilitation of task-relevant information processing after conflict trials seems too simple. This model in its current form cannot explain the interaction of compatibility level of the current and the preceding trial.

Models pointing to an important difference between adaptation to recent and adaptation to frequent conflict have been put forward recently. For instance, in the dual mechanisms of control theory (Braver, 2007; Braver, 2012) a proactive control mode is distinguished from a reactive control mode. It is argued that proactive control, i.e., sustained maintenance of task goals, needs more cognitive resources than reactive control which is triggered to refresh/reactivate task goals by certain stimuli. Transferred to interference tasks and adaptation to recent and adaptation to frequent conflict two control mechanisms seem possible in which one mechanism enforces a task-set (strategic adaptation to frequent conflict), whereas the other responds to changes in the need for cognitive control on a trial-by-trial basis (adaptation to recent conflict). This idea is comparable to the notion of micro- and macro-adjustments (Ridderinkhof, 2002).

One important hypothesis derived from dual mechanisms of control theory is that anxious people rely more on less demanding reactive control mechanisms than on more demanding proactive control mechanisms, because anxious people are occupied more by ruminations and worrying which consumes attentional resources. We tested this hypothesis in a behavioral experiment (see Chapter 4). Participants performed a Stroop-like in which conflict frequency was manipulated between task blocks. Participants were divided into two groups based on their scores in the state-trait anxiety inventory (Spielberger, Gorsch, Lushene, Vagg, and Jacobs, 1983). We found adaptation to recent conflict in the high anxious group only whereas both groups showed equal adaptation to frequent conflict. Although these results do not fit dual mechanisms of control theory without further assumptions, the results suggest that adaptation to recent and adaptation to frequent conflict are based on different cognitive mechanisms.

In the last experiment (see Chapter 5) we tried to replicate a recent study that found a simple dissociation between adaptation to recent and adaptation to frequent conflict (Mayr and Awh, 2009). In contrast to this study, we controlled the frequency of presentation for a subset of

stimuli to rule out practice effects for specific stimulus ensembles and effects of stimulus-response contingencies (Mordkoff, 1996, Wendt and Luna-Rodriguez, 2009). Participants performed a Stroop task and we manipulated the frequency of incompatible trials per block (50% in the first four and last four blocks, and alternating 70% and 30% in the middle eight blocks). A subset of incompatible and compatible trials was presented a fixed number of times and only this subset was used to test adaptation to recent and adaptation to frequent conflict effects. We found that modulation of the interference effect by recent conflict was confined to the beginning of the experiment (replicating Mayr and Awh, 2009). Nevertheless, in contrast to most studies Stroop interference in our study was higher after an incompatible trial. Most importantly, we found (normal) adaptation to frequent conflict, that can not explained by a reversed (or absent; last four blocks of the experiment) adaptation to recent conflict effect.

To summarize: Whereas prominent theories of cognitive control assume the same underlying mechanism for adaptation to recent and adaptation to frequent conflict, in this thesis I present four experiments suggesting that both effects are based on different mechanisms.

The results of this study have been published first in Purmann, S., Badde, S., Luna-Rodriguez, A., and Wendt, M. (2011). Adaptation to frequent conflict in the Eriksen Flanker Task: An ERP study. Journal of Psychophysiology, 25(2), 50.

2

Lack of Modulation of Early Visual ERP Components in Adaptation to Frequent Conflict

Modulation of early visual event related brain potentials have been observed with adaptation to recent conflict (Scerif, et al., 2006). Similar modulation would be expected with adaptation to frequent conflict, if adaptation to recent conflict and adaptation to frequent conflict were based on the same neurocognitive mechanism. In this experiment we therefore examined effects of adaptation to frequent conflict on early visual information processing. Participants performed a flanker task under conditions of varying conflict frequency. Scalp electroencephalogram (EEG) were recorded from the participants while they performed the task and early and late event-related potential components were examined. The posterior P1 to visual stimuli is thought to originate in extrastriate visual cortex and thus to reflect early visual information processing. Several studies have shown that spatial attention can modulate the amplitude of the posterior P1 to visual stimuli (e.g., Eimer, 1993; Eimer, 2000; reviewed in Martinez et al., 2001). The frontal N2 has previously been shown to be larger on incompatible than on compatible flanker task trials, presumably reflecting conflict from simultaneously active response tendencies (conflict monitoring hypothesis) or inhibition of a conflicting response (Aron, Robbins, and Poldrack, 2004; Kopp, Rist, and Mattler, 1996; Van Veen and Carter, 2002; Wendt, Heldmann, Muentz, and Kluwe, 2007). The P3 latency has been used as a measure of stimulus evaluation time, as its latency is modulated by stimulus determinability but not by difficulty of stimulus-response mapping (Dien, Spencer, and Donchin, 2004). It has been shown that the latency of the central P3 is prolonged for incompatible stimuli in the flanker task (e.g., Coles, et al., 1985; Heil, Osman, Wiegmann, Rolke, and Hennighausen,

Chapter 2. Lack of Modulation of Early Visual ERP Components in Adaptation to Frequent Conflict

2000; Kopp et al., 1996) indicating prolonged stimulus evaluation time for these stimuli. Two late ERP components were utilized to test predictions from the conflict monitoring model: The frontal N2, peaking between 240 and 320 ms, served as an indicator of response conflict, and the central P3, peaking around 420 ms, served as an indicator of stimulus evaluation time. It was expected to replicate previous findings for the N2 and P3, that is, a larger N2 amplitude and longer P3 latency for incompatible flanker trials compared to compatible flanker trials. Furthermore, the conflict monitoring model predicts that both effects were less pronounced under conditions of frequent conflict.

As regards the flanker task, variations of processing selectivity have traditionally been related to a zoom lens model of spatial attention (e.g., Eriksen and St. James, 1986; Eriksen and Yeh, 1985). That is, it is assumed that fluctuations in the magnitude of the flanker effect are mediated by adjusting the width of an attentional focus to larger or more constricted areas of space. Such adjustment is assumed to affect early stages of stimulus processing, enhancing stimulus information within the focus as a function of the degree of constriction. Although it seems straightforward to account for conflict-frequency-dependent modulations of the flanker effect in terms of such adjustments, it is also possible that frequent conflict affects later, response-related processes, such as altered stimulus-response translation or increased resolution of response conflict, rather than early stimulus processing. A zoom lens account of adaptation to frequent conflict predicts changes of early information processing stages. An early ERP component – the posterior P1, peaking around 100 ms, serving as an indicator for early sensory information processing – was utilized to test this prediction.

As a second strategy to find evidence for modulation of early visual information processing, a visual search task was inserted into blocks of flanker task trials. This method follows a procedure introduced by (LaBerge, 1983). To contrast spatial attention when participants responded to the meaning of a visually presented five-letter word versus the identity of its central letter, LaBerge inserted probe trials in which a target character was presented randomly at any of the five possible letter locations into blocks of word or letter classification trials. Whereas in the context of word classifications, probe RTs displayed a flat curve across target locations, in the context of letter decisions a marked center-to-periphery gradient occurred, that is, RTs increased with target eccentricity. This pattern of findings suggests that spatial attention was focused on the central letter location in the letter but not in the word task. Corroborating this result, (LaBerge and Brown, 1989) obtained steeper center-to-periphery slopes for various kinds of probe items in the context of attending to a central letter flanked on both sides by strings of alternating numbers (i.e., 8585S8585) than in the context of identifying a nine-letter word. In the probe task used in this experiment, participants made a discriminative response to a target stimulus which occurred unpredictably at the same location as the target stimulus in the flanker task or at one of the locations as the flankers in the flanker task. Applying the "early adjustment" idea to adaptation to frequent conflict, one would predict that visual information presented at the location of the target of the flanker task should be processed with increased efficiency under conditions of high conflict frequency, and thus responses to a target in the probe task occurring at this location to be facilitated. Whereas there should not

be an influence on stimulus processing in the probe task of the adjustment to frequent conflict in the flanker task, if this affects only later processing stages (late adjustment). Consistent with the latter view, it has been found that the effects of flanker distance and conflict frequency do not interact (Mattler, 2006). Increasing the spatial distance between target and flankers reduces the compatibility effect (Eriksen and Eriksen, 1974). As the distance effect has also – and more plausibly than the frequency effect – been related to a zoom lens model of spatial attention, both effects should interact, if the adaptation to frequent conflict also goes back to an adaptation of the focus of spatial attention.

2.1 Materials and Methods

2.1.1 Participants

Twelve (two female) university students at University of Hamburg participated. Age ranged from 22 to 38 years (mean = 25). By self report none of the participants had a history of psychiatric or neurological disorders. All participants had normal or corrected-to-normal vision and were naive with respect to the purpose of the study. Informed consent was obtained from each participant. Participants were either paid (€8 per hour) or participated for partial course fulfillment.

2.1.2 Design

Participants performed 20 blocks of 103 trials each. Most trials belonged to the flanker task. We manipulated the overall frequency of conflict between task blocks. In frequent conflict blocks 75% of all flanker trials were incompatible, while in infrequent conflict blocks only 25% of all flanker trials were incompatible. Conflict frequency was changed after every fifth block and was indicated to the participant by an instruction screen. The order of conditions was counterbalanced across participants. On average three flanker trials were followed by one trial of a probe task. Stimuli in both tasks were presented for 100 ms and the response-to-stimulus interval was fixed at 1,000 ms. An additional training block administered before the main part of the experiment was excluded from all remaining analyses.

Flanker Task

Triangles tilted to the right or to the left were used as stimuli and target and flankers were aligned vertically (cf. Kopp et al., 1996). On each trial a row of three vertically aligned equilateral triangles was presented at the center of the screen, extending approximately 5° of visual angle vertically and approximately 1° of visual angle horizontally. The central triangle – which was the target stimulus – was presented on the horizontal midline. Triangles could point to the left or to the right. On each trial, the left/right orientation of the target was chosen randomly. Left/right orientation of the flankers was chosen randomly within the constraints of

Chapter 2. Lack of Modulation of Early Visual ERP Components in Adaptation to Frequent Conflict

the compatible-to-incompatible trials ratio of the current experimental block. Responses were given by pressing two response keys which were mounted on an external rectangular keyboard (10 cm x 18 cm). The response keys extended 1.0 x 1.0 cm and were separated by 8.0 cm (parallel to the keyboard's long axis). Participants held the keyboard with both hands, roughly aligning its long axis with the vertical midline of the screen and tilting its upper end somewhat toward the screen. The lower key was pressed with the thumb of their right hand and the upper key was pressed with the thumb of the left hand. The bottom side of the keyboard was supported by the remaining fingers. A right-pointing target was assigned to the lower response key (right thumb) and a left-pointing target was assigned to the upper response key (left thumb). Probe Task Stimuli of the probe task were the digits 3 and 7. These stimuli were of equal size as the stimuli in the flanker task. On each probe task trial, either 3 or 7 occurred at one of the three possible locations (i.e., central, top, or bottom, randomly chosen) whereas the other digit was presented at both remaining locations. The digit which occurred only once served as target. Participants classified the target with the same two response keys used for the flanker task, pressing the lower key for 7 and the upper key for 3.

2.1.3 Procedures

Each participant came in for a single session which took three hours and included preparation for the EEG recording and performing the task. During the session participants sat in a comfortable chair in a dimly lit and sound attenuated room. The distance to the computer screen was approximately 100 cm. A standard PC running MS-DOS and in-house experimentation software was used to deliver stimuli and record responses. Another PC recorded the EEG. The EEG was recorded from 61 scalp electrodes (nonpolarizable Ag/AgCl electrodes) that were mounted at equal distance in an elastic cap (Easy Cap; FMS, Herrsching Breitbrunn, Germany; c.p. Figure 2.1 on page 25). Recordings were referred to the right ear lobe and an averaged left/right ear lobe reference was calculated off-line using the additional left ear lobe recording. Vertical eye movements were monitored (electrooculogram, EOG) with an electrode below the right eye against the reference. Horizontal eye movements were recorded with two electrodes placed at the outer canthi of each eye (bipolar recording). Electrode impedance was kept below 10 k Ω for all electrodes. Recordings were amplified (Synamps Amplifiers; Neuroscan, Sipplingen, Germany) in DC mode. The EEG and EOG were recorded continuously and digitized at 500 Hz. Preprocessing of the EEG recordings was performed with Brain Electric Source Analysis (BESA, <http://www.besa.de>) and included correction for eye movement and blink artifacts using BESA's PCA capabilities, lowpass (30 Hz) and highpass (1 Hz) filtering. All further analyses were conducted using custom Matlab (<http://www.mathworks.com>) scripts and EEGLAB (Delorme and Makeig, 2004) routines. The first three trials of each block were considered warm-up trials and not analyzed. Also data from all trials with an erroneous response and from trials following an erroneous response were excluded. To avoid confounding task-switching effects, flanker task trials following a probe task trial were excluded. Analyses of RTs were further confined to correct responses faster than 2,000 ms. For the ERP analysis epochs were calculated from 1,000 ms before stimulus onset to 1,000 ms after a stimulus. To

obtain baseline-corrected ERPs, the average voltage for the 100 ms preceding the stimulus was subtracted from the waveforms prior to all further analyses. Because the number of trials differed between conditions, an equal number of observations was created by randomly choosing trials out of the conditions with more trials. This procedure ensures equal signal-to-noise ratio between conditions. Then the epochs were averaged separately for each of the four conditions. To identify time intervals around each ERP component for each electrode the grand average over all participants and all conditions was calculated. For negative components the interval from the previous maximum to the next maximum was chosen. For positive component the interval from the previous minimum to the next minimum was chosen. To test the effects of conflict in the current trial and frequency of conflict on each component, the electrode on which the ERP component had its maximum/minimum in these grand averages was chosen.

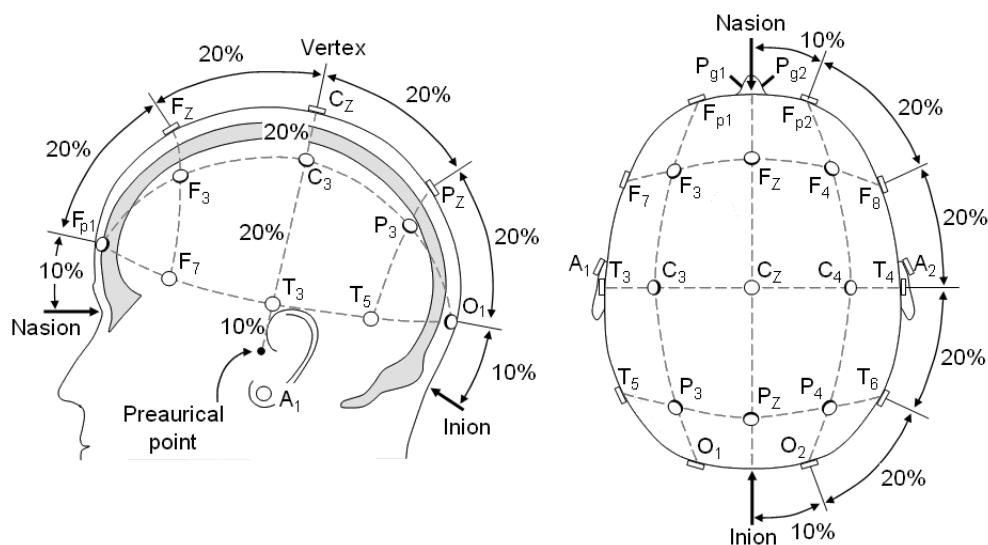


Figure 2.1: Electrode positions following the 10-20 system. We used a modified system with electrodes positions between these standard electrodes, such as CPz that was placed between Cz und Pz.

2.2 Results

2.2.1 Behavioral Data

Analyses of variance (ANOVAs) with the within-subject factors compatibility (compatible vs. incompatible) and conflict frequency (frequent vs. infrequent) were conducted on the mean RTs and the error rates. Incompatible trials were overall responded to more slowly and associated with more errors than compatible trials (460 vs. 391 ms, $F(1, 11) = 131.8$, $p < .01$; and 6.0% vs. 1.4%, $F(1, 11) = 19.1$, $p < .01$). This flanker effect was, however, modulated by the frequency of flanker-target conflict, $F(1, 11) = 92.7$, $p < .01$; and $F(1, 11) = 14.2$, $p < .01$, for RTs and error rates, respectively). In blocks involving 25% conflict trials performance on compatible and incompatible trials differed by 91 ms (385 and 476 ms, for compatible and

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incompatible trials, respectively) and 6.5% errors (1.3% and 7.8%, for compatible and incompatible trials, respectively). In blocks involving 75% conflict trials performance on compatible and incompatible trials differed by 47 ms (403 and 450 ms, for compatible and incompatible trials, respectively) and 2.9% errors (1.0% and 3.9%, for compatible and incompatible trials, respectively). Probe Task RTs for targets presented at the top, the central, and the bottom location were 699, 711, and 715 ms in the low conflict-frequency blocks and 704, 717, and 702 ms for the high conflict-frequency blocks. Neither the main effects of location and conflict frequency (both $F_s < 1$) nor the interaction, $F(2, 22) = 1.2, p = .31$, reached significance. Error rates for targets presented at the top, the central, and the bottom location were 8.4, 9.8, and 8.6% in the low conflict frequency blocks and 9.9, 8.4, and 10.7% for the high conflict-frequency blocks. Although this data pattern (i.e., a central advantage in high conflict-frequency blocks only) would be consistent with the early adjustment assumption, again neither the main effects (both $F_s < 1$) nor the interaction, $F(2, 22) = 2.3, p = .12$, reached significance.

2.2.2 Event-Related Potentials

Figure 2.4 on page 33 shows scalp maps for selected points in time. Figure 2.2 on page 28 shows stimulus-locked ERPs from midline electrode sites (Fz, FCz, Cz, CPz) of trials with compatible flankers (dotted line) and incompatible flankers (solid line) in infrequent conflict (left panels) and frequent conflict (right panels) blocks. At about 110 ms after stimulus onset an early negativity is evident. This component, labeled anterior N1, is followed by a fronto-central negativity N2 at around 280 ms. After the N2 a positivity, labeled central P3, is observed peaking around 400 ms post stimulus onset. Figure 2.3 on page 29 shows stimulus aligned ERPs at two occipital electrode sites with compatible flankers (dotted line) and incompatible flankers (solid line) in infrequent conflict (left panels) and frequent conflict (right panels) blocks. At about 100 ms after stimulus onset an early positivity, labeled posterior P1, is evident. After the P1 a negativity, labeled posterior N1, is observed, peaking around 175 ms post stimulus onset. For frontal effects, peak amplitude values were computed within three time windows. These time windows allowed us to reliably determine peak amplitude and peak latency for each participant. The first measurement interval was centered on the mean latency of the anterior N1 (90 - 180 ms post stimulus), the second latency window was centered on the mean latency of the fronto-central N2 (200 - 300 ms post stimulus), and the third latency window was centered on the mean latency of the central P3 (300 - 500 ms post stimulus). For posterior effects, peak amplitude values were computed within two time windows. The first measurement interval was centered on the mean latency of the posterior P1 (90 - 130 ms post stimulus) and the second latency window was centered on the mean latency of the posterior N1 (120 - 220 ms post stimulus). Peak amplitude for each electrode was measured relative to baseline and values obtained at the lateral posterior sites (P3, P4) and at midline electrodes (Fz, FCz, Cz, CPz) were submitted to separate analyses of variance (ANOVAs) with the factors compatibility and conflict frequency. Peak amplitudes and latencies are listed in Table 2.1.

Anterior N1

The N1 had a frontal scalp distribution. Inspecting Fz, FCz, and Cz the N1 was strongest at FCz (Fz = -2.9 μ V, FCz = -3.6 μ V, Cz = -3.2 μ V). Neither amplitude nor latency of any of the effects reached significance.

Fronto-Central N2

The N2 had a fronto-central scalp distribution and was most prominent on FCz (Fz = -2.3 μ V, FCz = -3.3 μ V, Cz = -3.1 μ V, CPz = -3.0 μ V). Although neither flanker compatibility nor conflict frequency showed an overall effect on peak amplitude, $F(1, 11) = 1.57, p = .24$ and $F(1, 11) = 0.47, p = .51$, respectively, the two factors interacted, $F(1, 11) = 15.0, p = .003$. Separate t-tests confirmed that a flanker effect in N2 amplitude, a greater peak amplitude for incompatible stimuli, was apparent only in the infrequent conflict blocks, $t(11) = 3.24, p = .008$, but not in the frequent conflict blocks, $t(11) = -0.80, p = .44$. There were no significant effects on peak latency.

Central P3

The P3 had a centro-parietal scalp distribution and was most prominent on CPz (Fz = 1.1 μ V, FCz = 2.6 μ V, Cz = 3.5 μ V, CPz = 4.0 μ V). Compatibility but not conflict frequency showed an overall effect on peak amplitude, $F(1, 11) = 5.11, p = .045$; $F(1, 11) = 0.21, p = .657$. Additionally, both factors interacted, $F(1, 11) = 10.47, p = .008$. Separate t-tests confirmed that a flanker effect in P3 peak amplitude, greater amplitude for compatible stimuli, was apparent only in the infrequent conflict block, $t(11) = 3.58, p = .004$, but not in the frequent conflict block, $t(11) = 0.64, p = .538$. Similar results were obtained for peak latency. Compatibility but not conflict frequency showed an overall effect on peak latency, $F(1, 11) = 13.11, p = .004$; $F(1, 11) = 0.17, p = .69$. Again, both factors showed a significant interaction, $F(1, 11) = 7.98, p = .017$. Separate t-tests confirmed that a flanker effect in P3 peak latency was stronger in the infrequent conflict blocks, $t(11) = 4.88, p < .001$, than in the frequent conflict blocks, $t(11) = 1.82, p = .095$.

Posterior P1

The P1 had a bilateral occipital scalp distribution. The posterior electrodes P3 and P4 were used to test attentional effects. For the P1 component, there was a main effect of electrode, $F(1, 11) = 15.44, p = .003$, a main effect of compatibility, $F(1, 11) = 5.68, p = .036$, and an interaction of electrode and compatibility, $F(1, 11) = 8.04, p = .016$, the latter reflecting that there was a compatibility effect on the right side, $t(11) = 3.20, p = .009$, but not on the left side, $t(11) = 0.21, p = .84$. No other effect was significant. Most importantly, the two-way interaction of compatibility, and conflict frequency, $F(1, 11) < 0.01, p = .99$, and the three-way interaction of electrode, compatibility, and conflict frequency, $F(1, 11) = 0.74, p = .41$, were far from significant. There were no significant effects on peak latency.

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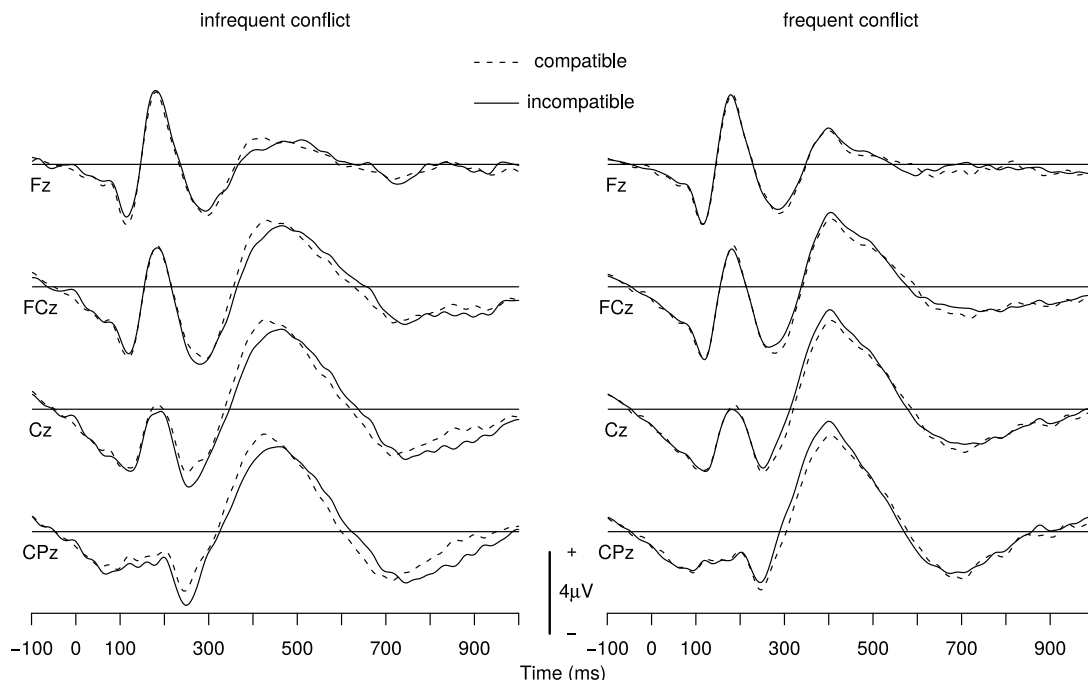


Figure 2.2: Stimulus-locked averaged waveforms over midline electrodes show increased amplitude of the N2 and increased latency of the P3 for incompatible trials in blocks with infrequent conflict trials.

Posterior N1

As none of the effects including electrode reached significance, we pooled electrodes P3 and P4 for the following analysis. Only compatibility showed a main effect on peak amplitude, $F(1, 11) = 7.57, p = .019$. Neither conflict frequency nor the interaction of the compatibility and conflict frequency was significant (both $F(1, 11) < 1$). There were no significant effects on peak latency.

2.3 Discussion

Adaptation to frequent conflict in a flanker task was examined using event-related brain potentials. Frequency of incompatible stimuli across task blocks were manipulated. It was expected to replicate previous findings on the fronto-central N2 and central P3. Other studies have shown an increased N2 amplitude and increased P3 latency for incompatible compared to compatible stimuli (e.g., Coles, Get al., 1985; Heil et al., 2000; Kopp et al., 1996). A prominent model of cognitive control (Botvinick et al., 2001) suggests the fronto-central N2 as an indicator of conflict monitoring. Based on this model it was predicted that the difference in N2 amplitude would be less pronounced under conditions of frequent conflict (high cognitive control). Flanker interference in terms of response times and error rates was reduced in blocks where conflict was frequent. The conflict-frequency modulation of flanker interference was

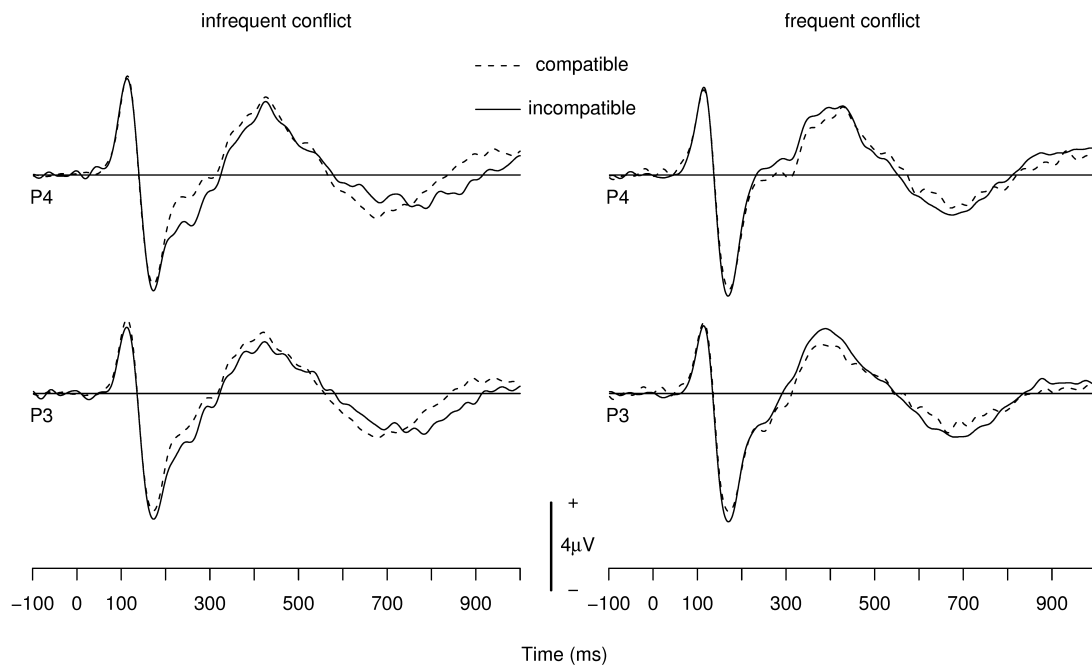


Figure 2.3: Stimulus-locked average waveforms over posterior electrodes show increased amplitude of the N1 for incompatible trials but no modulation of this effect by conflict frequency.

similar to that observed in previous studies (Gratton et al., 1992; Wendt and Luna-Rodriguez, 2009) and thus survived our manipulation of intermixing trials of a different task. The same conclusion can be derived from the psychophysiology data. Replication of findings concerning the fronto-central N2 was successful, in that N2 amplitude was greater for incompatible than for compatible flanker stimuli. As predicted, this difference in amplitude was reduced under frequent conflict, thus suggesting that incompatible flankers elicited less response conflict under conditions of frequent conflict. Also replication of findings concerning the P3 latency was successful. Latency of P3 was prolonged for incompatible stimuli, suggesting that our cognitive system needs more time to evaluate an incompatible stimulus. Again, the difference was reduced under conditions of frequent conflict, reflecting less influence of the task-irrelevant flankers on stimulus evaluation time when conflict is overall more frequent. Interestingly, a recent study also utilizing a flanker task found the opposite (Bartholow et al., 2005). They varied frequency of conflict trials across blocks, resulting in blocks with 80% incompatible trials (frequent conflict), blocks with 50% incompatible trials, and blocks with 20% incompatible trials (infrequent conflict). A difference in N2 amplitude for incompatible and compatible trials was evident only in the frequent conflict condition. While it can only be speculated about the reasons for these diverging results, a flanker effect in N2 amplitude in frequent conflict blocks only does not fit the conflict monitoring model (e.g., Botvinick et al., 2001; Van Veen and Carter, 2002).

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Table 2.1: Latency (ms) and amplitude (μV) of selected ERP components as a function of conflict frequency and compatibility of the current trial.

	electrode	Infrequent conflict		Frequent conflict	
		compatible	incompatible	compatible	incompatible
Amplitude					
Anterior N1	FCz	-3.3	-3.7	-3.5	-3.7
Fronto-central N2	FCz	-3.7	-4.4	-4.3	-4.0
Central P3	CPz	6.0	4.8	5.3	5.1
Posterior P1	P3/P4	3.7	4.0	3.9	4.2
Posterior N1	P3/P4	-5.7	-5.9	-5.3	-5.2
Latency					
Anterior N1	FCz	120	118	118	118
Fronto-central N2	FCz	256	263	264	263
Central P3	CPz	402	469	404	451
Posterior P1	P3/P4	115	116	116	116
Posterior N1	P3/P4	174	178	173	184

One problem for the interpretation of effects on the N2 and P3 is that both ERP components are commonly observed in combination and close temporal proximity (for a more detailed discussion on this issue see Folstein and Van Petten, 2008). It is likely that activity of the brain sources leading to deflections in the ERP overlaps in time. Therefore, observed changes in amplitude or latency of one component might result from changes in amplitude or latency of the other component, that is, N2 amplitude in trials with compatible flanker task trials might be decreased because of an earlier P3 or a P3 with smaller amplitude. Nevertheless, note that the predictions concerned both N2 and P3. Given the results of this study it can be assumed that at least one of these components (or to be more precise, their underlying neurocognitive processes) showed a decreased effect of compatibility level under conditions of frequent conflict. Another problem for the interpretation of effects on the N2 and P3 is that P3 amplitude (and also N2 amplitude) has been shown to increase with lower target probability in a visual search task (Luck and Hillyard, 1990) or for rare target stimuli in odd-ball tasks (Polich and Margala, 1997; effects on N2 are reviewed in Folstein and Van Petten, 2008). These effects are important to keep in mind because frequency of one class of stimuli has been manipulated, which might have odd-ball like influences on N2 and P3. Nevertheless, an odd-ball account of the amplitude effects can be ruled out. Within such an account the P3 amplitude for incompatible trials should be larger when incompatible trials are rare. The opposite was found: P3 amplitude was found to be larger for compatible trials under infrequent conflict (i.e., when compatible trials were frequent). Although only speculative, the effect on P3 amplitude might result from greater variability of P3 single-trial peak latency for incompatible trials,

which would result in reduced amplitude in the average waveform (cf. Roth, Roesch-Ely, Bender, Weisbrod, and Kaiser, 2008). It might be the case that frequent conflict leads to less variable P3 single-trial latencies, which makes the amplitude difference disappear in task blocks with frequent conflict. Corroborating this explanation, by visual inspection, the width of the P3 seems to be greater for incompatible stimuli in the infrequent conflict condition.

Traditionally, variations in processing selectivity in the flanker task have been related to a zoom lens model of visual attention. A zoom lens account would predict effects on early visual information processing. To test this prediction latency and amplitude of the posterior P1 ERP component was examined as an indicator for early (visual) information processing. Additionally, a zoom lens model of the conflict-frequency effect would predict generalization to other (visuospatial) tasks. To test this prediction, the effects of conflict frequency on a visual search task, which trials were intermixed within the flanker task trials, was examined. While the conflict manipulation seems effective in terms of behavioral data in the flanker task and effects on late ERP components, we did not observe conflict-frequency effects on the posterior P1 nor the posterior N1. Numerous studies have demonstrated that the amplitude of the posterior P1 and N1 are dependent on spatial attention (e.g., Clark and Hillyard, 1996; Hillyard and Anllo-Vento, 1998; Luck et al., 1994). For example, (Luck et al., 1994) employed cuing paradigms to manipulate participants' attention to particular spatial locations. Amplitudes for P1 and N1 were compared for attended versus unattended locations and for neutral trials, in which attention was more broadly focused. Unattended stimuli led to decreases in P1 amplitude, whereas attended stimuli led to increases in N1 amplitude. The missing modulation of the amplitudes of the posterior P1 and N1 by conflict frequency in our data does not support the idea of early adjustment to frequent conflict.

In this regard it is interesting to note that recent studies found conflict-frequency modulations to depend on irrelevant context material such as stimulus location. For instance, in one study participants had to classify the color of rectangles which were presented either above or below the center of the screen and were preceded by a centrally presented prime color word, which could match or mismatch the to-be-named color (Crump, Gong, and Milliken, 2006). Crucially, in that study the frequency of compatible and incompatible trials was varied in a location-specific manner. Stroop interference was significantly reduced for the location with frequent conflict compared to the location with infrequent conflict. In a similar vein, conflict-frequency-induced modulations of flanker interference have been found to depend on the frequency of conflict at specific stimulus locations (Corballis and Gratton 2003; see also Wendt, Kluwe and Vietze, 2008). Given other recent findings of context specificity of conflict-proportion-based conflict effects (e.g., Lehle and Hübner, 2008; Vietze and Wendt, 2009), it seems that attentional adjustment happens on the fly, i.e. on the basis of partial stimulus information rather than in advance of the imperative stimulus. Assuming that attentional adjustment does not start before encoding of certain general features of the stimulus/context which signal the appropriateness of attentional adaptation (in this case, for instance, whether the stimulus involves triangles or numbers) might account for (1) the lack of a difference in early evoked potentials (because adjustment has not taken place at this processing stage) and

Chapter 2. Lack of Modulation of Early Visual ERP Components in Adaptation to Frequent Conflict

(2) the lack of a conflict-proportion effect in the search task (because no adjustment occurs after identifying stimulus features which allow to classify the current trial as a search task which does not benefit from adopting the attentional strategy from the flanker task). Similar conclusions can be drawn from a lack of an enhanced advantage for central targets in the probe task in these frequent conflict blocks. Although one has to be careful in interpreting null results, the absence of an effect in the probe task does not agree with the assumption that adaptation to frequent conflict is based on a narrowing of the attentional focus. In contrast, these results fit well models that propose that attentional adaptation is context- or task-specific. For example, it has been found that modulations of interference related to conflict frequency operate in a task-specific manner (Fernandez-Duque and Knight, 2008). More precisely, intermixing trials of a color-word Stroop task and a number Stroop task, these authors found that increasing the frequency of conflict in one task reduced interference effects in this task only and left interference effects in the other task unaffected. As already pointed out in the General Introduction, the influence of task-relevant information on response selection could be increased (1) by facilitation of processing of task-relevant information, (2) by suppression of processing task-irrelevant information, (3) by facilitation and suppression, (4) by strengthening the coupling between the currently task-relevant information and the corresponding response (i.e., altering stimulus-response translation), or (5) by increased resolution of response conflict (i.e., concurrently activated response representations). The data presented here do not agree with any of the first three mechanisms. Furthermore, as modulation of early visual processing has been found for adaptation to recent conflict (Scerif, et al., 2006), the results presented here suggest that adaptation to frequent conflict is based on a different neurocognitive mechanism.

Importantly, in this study it is assumed that the effect of frequency of incompatible trials reflects cognitive control processes. Nevertheless, this effect might also be explained without the notion of cognitive control (Stürmer et al., 2002). Given that distractors co-occur with certain responses under conditions of frequent conflict, it was argued that the frequency modulation reflects associative distractor-response priming (which facilitates performance in incompatible trials when incompatible trials are frequent and performance in compatible trials when compatible trials are frequent) rather than an adjustment of processing selectivity. Obtaining a conflict-frequency effect in late ERP components but not in early components might also be consistent with this idea, if one still assumes that the fronto-central N2 reflects cognitive conflict. On the other hand, one would also expect to find odd-ball effects on the P3 (and N2), which was not found. To our knowledge no study investigating conflict-proportion effects seems to be able to dismiss such an associative account. Indeed, trying to examine attentional adjustment by means of a different task (involving different stimuli than the task associated with the conflict-frequency manipulation) seems to be a promising way (see Chapter 5). In sum, the results of this study suggest that conflict-frequency adjustments are task-specific, results either in more selective access of sensory information to response selection stages or in increased resolution of response conflict rather than in early filtering, and therefore differs from adaptation to recent conflict.

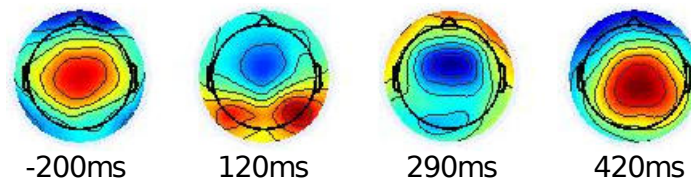


Figure 2.4: Scalp topography for selected points in time: 200 ms pre stimulus onset, 120 ms post stimulus onset, 290 ms post stimulus onset, and 420 ms post stimulus onset

The results of this study have been published first in Purmann, S., and Pollmann, S. (2015). Adaptation to recent conflict in the classical color-word Stroop-task mainly involves facilitation of processing of task-relevant information. Frontiers in human neuroscience, 9.

3

Modulation of Early Visual Brain Areas in Adaptation to Recent Conflict

Conflict adaptation theory proposes that adaptation to recent and frequent conflict is mediated by facilitation of early visual processes related to the relevant stimulus dimension. Nevertheless, it is important to note that cognitive control in each of these instances could be implemented in various ways: At the sensory level processing of task-relevant sensory information could get facilitated and/or processing of task-irrelevant sensory information could get suppressed. Furthermore, stimulus-response translation could be altered or, at the motor level, the response threshold could be increased. Finally, any mixture of these mechanisms seems possible. More globally, these adjustments seem to be accompanied by changes in representation of information higher-level areas. It has been shown that neurons in the frontal and parietal lobes represent stimulus features in an adaptive way based on current task demands (Woolgar, Hampshire, Thompson, and Duncan, 2011).

In this study, we aimed at specifying the neural mechanisms underlying this fine-tuning. Because in the connectionist model task-set implementation, adaptation to recent conflict and adaptation to frequent conflict are based the same neurocognitive mechanism it might be of value at this point to shortly review some brain imaging studies on on these effect. Studies on post-error adjustments are related as well, as these adjustments can be seen as another instance of trial-by-trial adaptation (Danielmeier and Ullsperger, 2011).

A limited number of studies have examined activation of brain areas involved in processing of the task-relevant and task-irrelevant stimulus dimensions in task-set implementation in

Chapter 3. Modulation of Early Visual Brain Areas in Adaptation to Recent Conflict

the Stroop and Stroop-like tasks. In some early functional imaging studies on the Stroop task, regional cerebral blood flow (rCBF) was measured using positron emission tomography while participants performed the classical Stroop task. These studies found either no evidence for enhancement of visual brain areas involved in color processing or suppression of left-hemisphere visual brain areas involved in word form processing (Pardo, Pardo, Janer, and Raichle, 1990; despite the fact that they specifically examined these areas), suppression in the extrastriate cortex (Bench et al., 1993), or an increase in rCBF in the left lingual gyrus and a decrease in left lateral extra-striate cortex (Carter, Mintun, and Cohen, 1995). Importantly, none of these studies localized visual color and word processing areas independently of the main task. In a more recent fMRI study, participants had to perform blocks of a Stroop task, with all stimuli being incompatible in some blocks and neutral in other blocks (Polk et al., 2008). For incompatible compared to neutral Stroop blocks they found increased activity in V4 and decreased activity in the VWFA and followed that both enhancement of processing of color information and suppression of processing of word information is part of task-set implementation. Taken together these studies suggest, that modulation of early visual areas might play a role in Stroop task performance and that this modulation might have the character of enhancement and/or suppression.

Given that all these studies on task-set implementation used block designs, none can separate transient (i.e., trial-by-trial) effects from sustained (i.e., block) effects. Therefore, it might be that the reported enhancement or suppression (Polk et al., 2008) are due to trial-by-trial conflict adaptation effects, as incompatible trials that followed incompatible trials occurred in incompatible Stroop blocks only.

An fMRI study on adaptation to recent conflict explicitly tested if this effect is mediated by enhancement of processing of task-relevant information, suppression of processing of task-irrelevant information, or by both (Egner and Hirsch, 2005). In this fMRI study a face-word Stroop task was used. In some blocks participants had to respond to the faces, in others they had respond to the words. Behaviorally, they found interference and conflict adaptation effects under both task-sets. For incompatible trials following incompatible trials enhanced activity in the FFA was found, if faces were the task-relevant information, but not when faces represented the task-irrelevant information. They concluded that enhancement of task-relevant sensory information processing is the primary mechanisms of conflict resolution. Nevertheless, the results have to be interpreted carefully. In contrast to the classical Stroop task, where there is only one stimulus (with two stimulus dimensions), in the face-name Stroop task there are two stimuli. It is known that interference effects under such conditions are smaller (MacLeod, 1991), pointing to differences in the neurocognitive mechanisms between Stroop-like tasks using integrated and non-integrated stimuli. If effects found in one task generalizes to the other is currently not known. Additionally, in the experimental design they used, participants had to switch between face discrimination and word discrimination in a block-wise fashion. This manipulation was necessary to be able to examine activity in the FFA under two conditions, when faces were task-relevant and task-irrelevant, respectively. While a reverse Stroop-effect has been described, observing interference effects under both task-sets

is unusual. It is known that switching between two task-sets in a block-wise fashion can lead to carry-over effects from one block to another (Allport et al., 1994; Allport and Wylie, 1999; Monsell, 2003). This task-set inertia could possibly explain the observed behavioral results, nevertheless, how task-set inertia effects interact with conflict adaptation effects is currently not well understood.

In an ERP study on adaptation to frequent conflict, no modulation of early sensory components by conflict frequency has been found (Purmann, Badde, Luna-Rodriguez, and Wendt, 2011; see Chapter 2). In this study, frequent conflict was associated with reduced flanker interference in response times and error rate. The amplitude of the fronto-central N2 was larger and latency of the central P3 longer for incompatible stimuli and both effects were smaller when conflict was frequent. Most interestingly, neither amplitude nor latency of the posterior P1, as index of early visual processing, was modulated by conflict frequency, suggesting that adaptation to frequent conflict is not mediated by enhancement or suppression of sensory information processing but by adjustments at a later stage of information processing.

In a recent fMRI study on post-error adjustments using a face Simon task, post-error slowing was accompanied by BOLD activation of a network resembling response inhibition and suppression of somatomotor cortex, and post-error reduction of interference was accompanied by enhancement of activity in the FFA (King et al., 2010), showing that both, enhancement of task-relevant information processing and adjustment of the response threshold are mechanisms recruited in response to error trials. As already noted, adjustment of the response threshold might also play a role in conflict adaptation (Gratton et al., 1992).

Although it is plausible (and most parsimonious) to assume that the mechanisms underlying implementation of a task-set, adaptation to recent conflict, adaptation to frequent conflict, and post-error adjustments are the same, there is not much evidence for this assumption so far. Quite to the contrary, evidence is emerging that raises doubt on this assumption. Additionally to the similarities and differences already mentioned, it has been found in behavioral studies that while frequency effects can be shown in an early phase of motor responses (i.e., movement initiation), recency effects seem to be confined to later phases (Purmann et al., 2009), recency effects disappeared after controlling for feature integration effects but frequency effects were still present (Fernandez-Duque and Knight, 2008), and that while recency effects vanished over the course of the experiment, frequency effects can be found over the whole course of the experiment (Mayr and Awh, 2009).

In our study we measured the blood-oxygenation level dependent (BOLD) response using magnetic resonance imaging while participants performed a color-word Stroop task (Stroop, 1935). The Stroop task is one of the interference tasks most often used to study selective attention and cognitive control in the laboratory (for a review see MacLeod, 1991), so the neural underpinnings of cognitive processes involved in this task will be of interest to a broad readership. To examine if adaptation to recent conflict involves enhancement or suppression of sensory information processing, we identified inferotemporal brain regions involved in

Chapter 3. Modulation of Early Visual Brain Areas in Adaptation to Recent Conflict

color (visual areas V4 and V4 α ; cf. Bartels and Zeki, 2000) and word processing (visual word form area/VWFA; cf. Cohen et al., 2000; Reinholz and Pollmann, 2005; but see also Price and Devlin, 2003) in independent localizer tasks. We used activity in these relatively well-understood, functionally defined brain regions as indicators for early sensory information processing of task-relevant and task-irrelevant information, respectively. Increases of activity in V4/V4 α after a conflict trial would lend support for an enhancement model, a reduction of activity in VWFA would support a suppression model, while a combination of activation increase in V4 and reduction of activity in VWFA would support a dual-mechanism model. No modulation of sensory brain areas while seeing conflict adaptation effects in behavior would speak for modulation at later processing stages such as changing stimulus-response translation or adjustment of the response-threshold of the motor system.

When investigating adaptation to recent conflict, it is crucial to control for the sequence of stimulus features (e.g., colors and words) and responses. In standard paradigms (i.e., using limited sets of stimuli and responses), repetitions of the compatibility level (i.e., a compatible trial following a compatible trial or an incompatible trial following an incompatible trial) tends to be associated with either repetition or alternation of both the target and the distractor information. Compatibility level alternations, on the other hand, tend to be associated with repetition of either the target or the distractor information and alternation of the other (i.e., partial feature repetition). According to event file theory (Hommel, 2004), partial feature repetitions are associated with a processing disadvantage because of a mismatch between the prior processing episode and the current task demands. It is therefore possible that reductions of interference effects after conflict trials reflect such processing disadvantages rather than an adjustment of selectivity of information processing (Notebaert, Gevers, Verbruggen, and Liefoghe, 2006). To control for feature-integration effects, we applied a 6:6 mapping between colors and responses and created pseudo-random stimulus-sequences that only included complete alternations of stimulus features from one trial to the next. More specifically, no color reoccurred as color or word on the next trial and no word reoccurred as color or word on the next trial. Another method to deconfound feature-integration and conflict adaptation effects is to exclude partial and/or complete repetitions from the analysis (e.g., Kerns et al., 2004) but lead to a substantial loss of data. Importantly, feature-integration and conflict adaptation effects has successfully been deconfounded by the described methods (for an example in the Eriksen flanker task see Wendt, Kiesel, Geringswald, Purmann, and Fischer, 2014).

3.1 Materials and Methods

3.1.1 Participants

We recruited 20 students from the population of students of the University of Magdeburg. Data from two participants had to be excluded from the analysis, one because of an imaging artifact and one because of technical problems in collecting the behavioral data, resulting in a

final sample of 18 students. Eight participants were male and age ranged from 20 to 29 (mean = 24). Vision of all participants was normal or corrected to normal and none of the participants reported any neurological or psychiatric abnormality or conditions contraindicating MRI. Additionally, by self report none of the participants was color blind, all participants had a right hand preference and were native German speakers. Participants were paid or participated for partial course fulfillment. The experiment was carried out in accordance with the Declaration of Helsinki.

3.1.2 Experimental Paradigms

Participants performed three different tasks: One task used to localize visual areas relevant for color processing, one task used to localize brain areas relevant for word processing and a color word Stroop task (Stroop, 1935).

Color localizer task. Participants performed a task similar to the Farnsworth-Munsell 100-Hue Test ((Beauchamp, Haxby, Jennings, and DeYoe, 1999)). This task has been found to reliably activate inferotemporal brain regions related to color processing. Participants saw a series of displays that were block-wise either achromatic (non-color condition) or chromatic (color condition). Each display was composed of an array of five wedges arranged in a circular fashion around a fixation cross presented at the center of the screen. These wedges could form a continuous sequence or include one wedge that did not fit in. Participants had to decide, if the sequence was continuous or not and give their answer by pressing a button with their right or left index finger, respectively.

Word localizer task. Participants performed a one-back memory task. Four-letter words with comparable frequency (Institut für Deutsche Sprache, 2009; word condition) and four-digit numbers (non-word condition) were used as stimuli (c.p. Park, Hebrank, Polk, and Park, 2012). Participants saw a series of either words or numbers in a block-wise fashion and had to indicate any direct repetition of a word (or number) by pressing a button with their right index finger and a change by pressing a button with their left index finger.

Stroop task. Color words (blue, red, green, yellow, orange, violet) printed in different colors (blue, red, green, yellow, orange, violet) were presented above a fixation mark. Participants had to indicate the font color by pressing one of six buttons. For ease of task performance, response-to-button mappings were presented at the bottom part of the screen, and participants were trained prior to the fMRI session. Participants used the index, middle and ring fingers of their right and left hands for responding. Response-to-button mappings were randomly assigned to participants. In compatible trials, word meaning and word color were the same. In incompatible trials, word meaning and word color differed. Compatible and incompatible trials were presented with equal probability.

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For all tasks, participants were instructed to keep their eyes on the fixation cross and to respond as fast as possible while trying to keep the error rate between five and ten percent. Mean response time and error rate were provided as feedback after each Stroop fMRI run.

Overall, participants performed seven runs of 7–8 min each: Two color localizer runs, two word localizer runs, and three Stroop runs. During a word localizer run participants performed eight task blocks, 29 s in length. In each task block, 20 displays were presented, each for 500 ms and an inter-stimulus-interval of 1000 ms. There was a fixation interval of 20 s between blocks. During a color localizer run participants performed eight task blocks, 29 s in length. In each task block, 10 displays were presented, each for 2000 ms with an inter-stimulus-interval of 1000 ms. There was a fixation interval of 20 s between blocks. During a Stroop run, participants performed 100 trials. Trials were jittered with a mean inter-trial-interval of 2.5 s. At the beginning of each trial the fixation cross disappeared for 200 ms (warning signal), after another 300 ms the stimulus was presented for 400 ms. Each participant started with a localizer run (color or word localizer, randomized between participants), continued with a Stroop run, after which localizer and Stroop runs alternated.

3.1.3 Analysis of Behavioral Data

Median RTs (Ratcliff, 1993) and arcsine square-root transformed error rates were analyzed using separate repeated-measures analyses of variance (ANOVA). All RT analyses excluded error trials and trials immediately following errors and trials, in which participants did not respond. Arcsine square-root transformed error rates were used to normalize the data due to a positive skew frequently associated with error-rate data (Neter, Wasserman, and Kutner, 1985).

3.1.4 MRI Data Acquisition and Analysis

Magnetic resonance imaging was performed on a 3T Siemens Trio MRI scanner with an 8-channel head coil. For functional imaging we used a T2*-weighted BOLD sensitive gradient echo echo-planar imaging (main task: TR = 2000 ms, TE = 32 ms, FA = 80, FOV = 19.2 cm, MAT = 64 × 64, 3 mm × 3 mm × 3 mm, 1 mm inter-slice gap, interleaved acquisition, 32 slices; localizer tasks: TR = 1500 ms, TE = 32 ms, FA = 80, FOV = 19.2 cm, MAT = 64 × 64, 3 mm × 3 mm × 3 mm, 1 mm inter-slice gap, interleaved acquisition, 24 slices). For the main task whole brain was covered, for the localizer task only the occipital, temporal and ventral frontal lobes were covered. The first 10 s of each run were discarded to allow for steady-state tissue magnetization. Prior to collection of functional data, T1-weighted anatomical images in the same plane as the functional images were acquired using a gradient-echo multi-slice sequence. High resolution T1-weighted Fast Low Angle SHot (FLASH; TR = 30 ms, TE = 4.4 ms, FA = 80, FOV = 19.2 cm, MAT = 64 × 64, 176 axial slices, resolution of 1 mm × 1 mm × 1 mm) anatomical images were collected at the end of the session to allow for localization and visualization of brain activation. Head motion was restricted using foam padding that surrounded the head. We back-projected the stimuli onto a screen, which was positioned behind the head coil. Subjects viewed this

screen through a mirror attached to the head coil. Presentation®software (Neurobehavioral Systems, <http://www.neurobs.com>) was used to present stimuli and to collect responses.

Preprocessing

All functional MRI analyses were carried out using FSL 5.0 (Smith et al., 2004). Images were corrected for slice time differences and small head movements (Jenkinson, Bannister, Brady, and Smith, 2002). Translational movement parameters never exceeded one voxel in any direction for any subject. During preprocessing, we applied spatial smoothing using Gaussian kernels of FWHM 6 mm as well as multiplicative mean intensity normalization of the volume at each time point and high pass temporal filtering (160 s).

Univariate analysis

First Level Analysis. Localizer tasks. The localizer tasks resembled a block design and were analyzed accordingly. Two boxcar functions, each representing one condition (color vs. non-color, word vs. non-word, for the two localizer tasks respectively) were convolved with a double gamma function and fed as regressors into the general linear model (GLM). Additionally, six motion parameters estimated during preprocessing were included in the GLM as nuisance regressors. The GLM used a local autocorrelation correction (Woolrich, Ripley, Brady, and Smith, 2001).

Stroop task

The Stroop task resembled an event-related design and was analyzed accordingly. Within the general linear model framework, a model with four regressors of interest, one for each trial type (cC, cI, iC, iI; the lower case letter denotes conflict level of the previous trial and the upper case letter conflict level of the current trial), was calculated. Each regressor consisted of a series of impulse functions (50 ms), positioned at trial onset. These regressors were convolved with a double gamma function. Additionally, six motion parameters estimated during preprocessing, regressors for error trials and the first derivative of regressors of interest were included in the GLM as nuisance regressors. The GLM used a local autocorrelation correction (Woolrich et al., 2001).

Second level and group analysis

After statistical analysis for each single run, the resulting statistical images were normalized into common stereotactic space with isotropic voxels of $1 \times 1 \times 1$ mm size, before the three runs of each participant were combined in subject-specific fixed-effects analyses. Results of this second level analysis were then fed into a random-effects group analysis. This analysis resulted in Z-statistic images. Normalization involved three steps: Registration of the average func-

tional image to the low-resolution structural image, of the low-resolution structural image to the bias corrected high-resolution structural image, and of the bias corrected high-resolution structural image to the MNI T1 template. The different coregistration matrices were then combined to normalize statistical images resulting from the first level single subject analysis into MNI space. To correct for multiple comparisons in whole brain analyses we only retained clusters that exceeded a minimal size. These minimal cluster sizes were determined using Monte-Carlo simulations as implemented by AlphaSim (AFNI, <http://afni.nimh.nih.gov/>) and result in an overall $p < 0.05$ whole brain. Specific cluster sizes are given in the relevant parts.

Identification of regions of interest

For each participant we identified four regions-of-interest (ROIs) for color processing restricted by anatomical and functional constraints. We created anatomical masks from a probabilistic atlas (Harvard-Oxford cortical structural atlas, Desikan et al., 2006) for the occipitotemporal fusiform gyrus ($V4\alpha$) and the occipital fusiform gyrus ($V4$) for each hemisphere (c.p. Beauchamp et al., 1999; Bartels and Zeki, 2000). For each participant we then determined the peak voxel in the color vs. non-color contrast in these individual anatomical ROIs and calculated the median percent signal change for a sphere of 60 voxels (radius = 15 mm, volume = 2160 mm³) around these peak voxels.

For each participant we identified a ROI for word processing restricted by anatomical and functional constraints. We created anatomical masks from an probabilistic atlas (Harvard-Oxford cortical structural atlas, Desikan et al., 2006) for the posterior temporal fusiform gyrus (VWFA; c.p. Cohen et al., 2000; McCandliss, Cohen, and Dehaene, 2003; Reinholz and Pollmann, 2005). For each participant we then determined the peak voxel in the word vs. non-word contrast in these individual anatomical ROIs. We used a sphere of 60 voxel (radius = 15 mm, volume = 2160 mm³) around these peak voxels as our ROIs for the main analysis.

Because the inferotemporal cortex is prone to signal dropout effects due to its proximity to the ear canal, we also calculated temporal signal to noise ratio (TSNR) for these regions for each of the seven fMRI runs for each subject to ensure that the signal in our ROIs allows robust statistical analysis (Murphy, Bodurka, and Bandettini, 2007).

3.2 Results

3.2.1 Behavioral Results

We calculated a repeated measures ANOVA with median RT as dependent variable and conflict in the preceding trial (incompatible vs. compatible) and conflict in the current trial (incompatible vs. compatible) as independent variables. There was a main effect of conflict in the current trial [Stroop effect; $F(1, 17) = 101.9$, $p < 0.001$], reflecting that overall response times were longer for incompatible (895 ms) than for compatible (782 ms) trials. There was also

Table 3.1: Recency effect in Experiment 3: Response times (and standard deviation) in ms and error rates in percent.

	current trial			
	compatible		incompatible	
preceding trial	RT	ER	RT	ER
compatible	779 (127)	2.4	907 (140)	5.1
incompatible	785 (121)	1.4	883 (126)	5.3

an interaction effect between conflict in the current trial and conflict in the previous trial [conflict adaptation; $F(1, 17) = 8.1, p < 0.05$], reflecting that Stroop interference was smaller after an incompatible trial (98 ms) than after a compatible trial (128 ms). No other effects were significant. We present data in Table 3.1.

We calculated a repeated measures ANOVA with arcsine square-root transformed error rates as dependent variable and conflict in the preceding trial (incompatible vs. compatible) and conflict in the current trial (incompatible vs. compatible) as independent variables. There was a main effect of conflict in the current trial [Stroop effect; $F(1, 17) = 29.0, p < 0.001$], reflecting that error rates were higher for incompatible (5.2%) than for compatible trials (1.8%). No other effects were significant. Although there was a conflict adaptation effect in response times only, the pattern of error rates excludes speed-accuracy trade-off as a possible explanation for this pattern of response times (see Table 3.1).

3.2.2 Neuroimaging Results

Color Localizer. At the individual level all participants showed a clear pattern of activation. In each participant we found greater activation in an anterior and a posterior part of the fusiform gyrus in both hemispheres for color blocks compared to non-color blocks (see Figure 3.3 on page 51 for a representative example). Data for peak voxels can be found in Table 3.2. Peak voxel coordinates are highly consistent with what has been found in other studies (c.p. Beauchamp et al., 1999; Bartels and Zeki, 2000).

Word Localizer. In each participant we determined the peak voxel in the posterior part of the temporal fusiform gyrus in the left hemisphere for word blocks compared to non-word blocks. Data for peak voxels can be found in Table 3.2 and data of a representative subject is presented in Figure 3.4 on page 51. These coordinates are consistent with what has been found in other studies, although the activation in our study is more anterior to studies that contrasted letter string and pseudowords with similar complex symbol strings (c.p. Cohen et al., 2002; MNI $x = 43, y = 54, z = 2$). Nevertheless, our results replicate the localization that has been found in a recent study when contrasting letter strings with number strings (Park et al., 2012; MNI $x = 36, y = 37, z = 23$).

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Table 3.2: Median and range of activation and MNI coordinates for peak voxels of inferotemporal regions of interest.

	Z_{max}	x	y	z	TSNR
<u>left hemisphere</u>					
V4	6.2 3.64 to 9.67	-30 -37 to -15	-73 -87 to -61	-11 -19 to -5	64
V4 α	6.2 2.98 to 10.22	-29 -40 to -23	-55 -64 to -42	-13 -20 to -8	57
VWFA	4.2 1.98 to 7.93	-39 -46 to -21	-32 -45 to -11	-20 -33 to -15	50
<u>right hemisphere</u>					
V4	6.3 2.64 to 10.15	31 26 to 37	-70 -81 to -61	-11 -17 to -5	62
V4 α	6.1 3.52 to 9.03	29 23 to 40	-47 -58 to -37	-17 -26 to -8	50

Table 3.3: Stroop task: Incompatible vs. compatible trials ($z > 3.1$, $p < 0.05$ with clustersize $> 878 \text{ mm}^3$).

	volume	Z_{max}	x	y	z
<u>right hemisphere</u>					
Insular Cortex	1779	3.83	42	13	-5
Precentral Gyrus	2036	3.98	48	8	22
<u>left hemisphere</u>					
Inferior Frontal Gyrus	5698	5.06	-44	9	6
Precentral Gyrus	1433	4.27	-32	-8	56
Superior Parietal Lobule	7146	4.59	-30	-51	42
<u>midline</u>					
Paracingulate Gyrus	3030	4.4	1	12	48
Precuneus Cortex	1290	3.88	-4	-60	44

Stroop Task. To validate our data we first tried to replicate results found in the Stroop literature. When contrasting incompatible with compatible trials (see Table 3.3 and Figure 3.5 on page 52), we found increased activity for the posterior medial frontal gyrus (pmFG; Figure 3.5A), inferior frontal gyrus (IFG; Figure 3.5B), and superior parietal cortex (Figure 3.5C), consistent with previous studies (e.g., MacLeod and MacDonald, 2000; Laird et al., 2005; Nee, Wager, and Jonides, 2007).

Region of Interest Analyses. Most important for our research question, we analyzed the activation pattern in early visual brain areas during performance of the Stroop task to examine modulation of sensory representations. While we were able to replicate previous studies in our whole brain analysis, whole brain analyses are in general considered often not to be sensitive enough to reveal modulation of small regions of interest for which additionally high inter-individual variability in exact anatomical location exists.

Percent signal change was calculated for V4 and V4 α (i.e., color processing ROIs) and VWFA (i.e., word processing ROI) for each participant to examine whether activity in task-specific sensory areas shows enhancement and/or suppression as a function of conflict of the preceding trial.

To analyze activity in color processing ROIs we calculated a repeated measures ANOVA with percent signal change as dependent variable and conflict in the preceding trial (incompatible vs. compatible), conflict in the current trial (incompatible vs. compatible), hemisphere (left vs. right), position (anterior [V4 α] vs. posterior [V4]) as independent variables for the four color processing ROIs. Except for the interaction-effect of conflict in the previous and conflict in the current trial [$F(1, 17) = 6.07, p = 0.025$] none of the effects were statistically significant. We therefore pooled data of all four color ROIs for subsequent analyses. Separate t-tests showed that there was greater activity for incompatible trials that were preceded by an incompatible trial compared to those that were preceded by a compatible trial [$t(17) = 2.51, p = 0.022$] and greater activity for incompatible trials compared to compatible trials when preceded by an incompatible trial [$t(17) = 2.67, p = 0.016$] but not when preceded by a compatible trial ($p = 0.18$). No other effects were significant (see Figure 3.1). As a side note, it is interesting not to find an effect for position, i.e., no difference between V4 and V4 α . Activation of V4 has been reliably found in passive viewing of color stimuli, activation of V4 α is reliably seen in tasks requiring active manipulation of color information (Beauchamp et al., 1999). In another fMRI study V4 α but not V4 showed activation during memory retrieval for color stimuli (Slotnick, 2009). Therefore, one might have suspected to find a stronger effect for V4 α than for V4.

To analyze activity of the word processing ROI we calculated a repeated measures ANOVA with percent signal change as dependent variable and conflict in the preceding trial (incompatible vs. compatible) and conflict in the current trial (incompatible vs. compatible) as independent variables. Except for the main effect of conflict in the current trial [$F(1, 17) = 9.45, p = 0.007$], reflecting that BOLD activity was greater for incompatible trials than for compatible trials, none of the effects were statistically significant (see Figure 3.2).

3.3 Discussion

Selectivity of information processing and adaptation thereof are key cognitive abilities for successful behavior in everyday life. To study these abilities in the laboratory, often so called interference tasks are used. Participants in these experiments are thought to enter a task-dependent cognitive set that is maintained for the duration of the task (Logan and Gordon, 2001), while information processing is fine-tuned on a short temporal scale to optimize

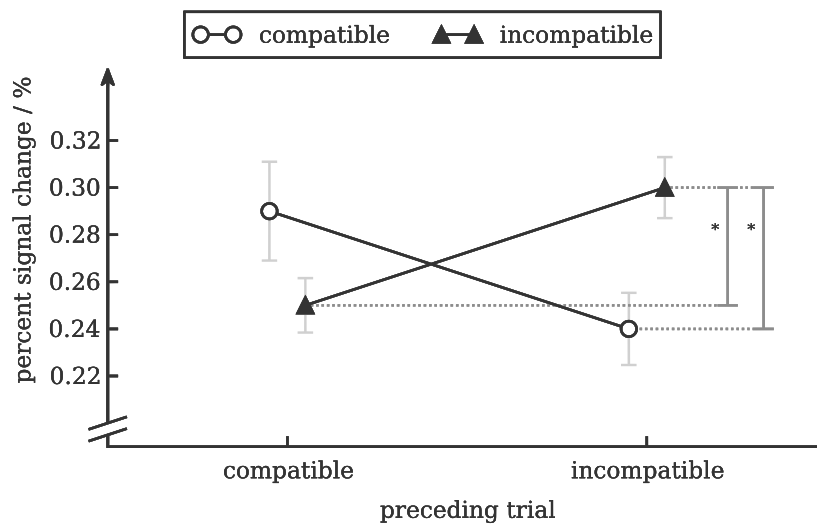


Figure 3.1: Percent signal change in V4/V4 α as a function of conflict in the previous and current trial. Error bars show standard error of the mean.

task performance (Gratton et al., 1992). In this study, we aimed at specifying the neural mechanisms underlying this fine-tuning. Participants performed the Stroop task while BOLD signal was measured with fMRI. To exclude non-attentional accounts of the conflict recency effect (Hommel, 2004) we carefully controlled stimulus sequences. As in a recent study, we used an extended set of stimuli and responses to deconfound non-attentional sequential effects and conflict adaptation (Wendt et al., 2014).

Current models of cognitive control account for conflict adaptation effects by assuming attentional adjustment, i.e., fine tuning of selectivity of information processing, in response to cognitive conflict. One account supposes that the main mechanism of conflict adaptation involves adjustment of the response threshold (Gratton et al., 1992). In this model the cognitive system can give a response during an early (parallel) phase or a later (focused) phase in information processing. While during the parallel phase the cognitive system cannot distinguish between task-relevant and task-irrelevant information, during the focused phase it can. Giving a response during the parallel phase will lead to fast and correct responses for compatible trials and fast but wrong responses for incompatible trials, as it is assumed that the task-irrelevant information has a stronger impact on response selection during this phase. Giving a response during the focused phase on the other hand will lead to slower but correct responses for both compatible and incompatible trials. During the parallel phase only because of interruption of motor response execution and reprogramming of the motor response can a correct response be given for incompatible trials, which slows down response times substantially for such trials and puts them even at a disadvantage compared to responses given during the focused phase, for which this interruption and reprogramming is not needed. Conflict adaptation then is thought about as switching from selecting the response during the parallel phase to selecting the response during the focused phase. While adjustments might occur at the response level (see also King et al., 2010), given our data we have to state that modulation of sensory process-

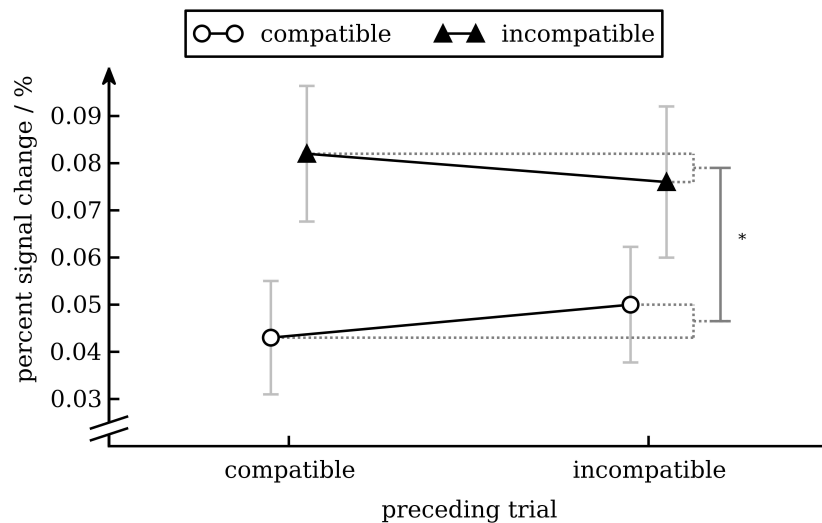


Figure 3.2: Percent signal change in the VWFA as a function of conflict in the previous and current trial. Error bars show standard error of the mean.

ing seems to be important too and is not included in this model. Another account assumes that adaptation to recent conflict is realized by enhancement of processing of task-relevant information early in information processing. This parallel distributed processing (PDP) model of the Stroop task (Cohen et al., 1990) proposes input units, that process task-relevant and task-irrelevant sensory information, response units, that plan and execute motor responses, and task demand units, that represent task rules and bias input units for successful task performance. A specific task-set (e.g., color-naming) is implemented by enhancement of processing of task-relevant information. The model has been extended (Botvinick et al., 2001) to account for adaptation to recent (Gratton et al., 1992) and frequent (Logan and Zbrodoff, 1979) conflict by adding a conflict monitoring unit. Concurrent activation of response units is used as a measure of response conflict and continuously signaled to a task-demand module which in turn enhances processing of task-relevant information and thereby increases selectivity of information processing. In this way, the current task-set is strengthened after an incompatible trial (recency effect) and this effect adds up, when incompatible trials occur often (frequency effect). More specifically, in this model the task-demand units increase activity of task-relevant input units when conflict is high, leading to reduced interference in the following trial and when conflict is frequent.

In the whole-brain analysis we found increased activity in a fronto-parietal network for incompatible trials compared to compatible trials, consistent with the literature (e.g., MacLeod and MacDonald, 2000; Laird et al., 2005; Nee et al., 2007). As these regions have been found to be activated also by other interference paradigms than the Stroop task, they are thought to be involved more generally in the detection and resolution of cognitive conflict (Wager et al., 2005; Nee et al., 2007). It has been shown, that these areas can adaptively represent task-relevant information (adaptive coding; see Woolgar et al., 2011). Most importantly with respect to

Chapter 3. Modulation of Early Visual Brain Areas in Adaptation to Recent Conflict

our research question, we found modulation by recent conflict of early sensory processing. This modulation was found in V4, an area that supports processing of the task-relevant stimulus color but not in the VWFA, an area that supports processing of the task-irrelevant word information.

It is interesting that after an incompatible trials activity in V4 increased only for incompatible trials but not for compatible trials, as from a simple enhancement model (upregulation of V4 after an incompatible trial) one would expect an equal increase in BOLD activity for compatible and incompatible trials (i.e., a main effect of conflict in the previous trial). Our results show that activity in V4 can be modulated by conflict in the current trial (likely through top-down control after the cognitive system has identified the compatibility level of the current stimulus). In our study this modulation occurs in a state of heightened cognitive control (i.e., after an incompatible trial) only. One interesting aspect of our data is that BOLD activity in V4 for cC trials was as high as for iI trials (see Figure 3.1). How this pattern evolves remains unclear. Nevertheless, this pattern has also been observed in another study (Egner and Hirsch, 2005), demonstrating its robustness. Importantly, activity for incompatible trials was greater after an incompatible trial than after a compatible trial, replicating results from the aforementioned study (cp. Figure 2D in Egner and Hirsch, 2005). With respect to modulation of processing of task-irrelevant information, if anything one would expect decreased activity in the VWFA for incompatible trials. Interestingly, we actually observed increased activity for incompatible trials. Given that activity in VWFA was not modulated by conflict in the previous trial, the main effect of conflict in the current trial might simply reflect a time-on-task effect: As response times for incompatible trials were longer than for compatible trials, the VWFA was used for a longer period of time on these trials. Therefore, this effect might not reflect attentional modulation specific to incompatible trials (Weissman and Carp, 2013). Note that the same argument cannot be made for V4: there was no main effect of trial compatibility, but an interaction between current and previous trial compatibility.

Our results fit an ERP study that also found modulation of early visual processing after incompatible trials (Scerif et al., 2006). Interestingly a related fMRI study on task-set implementation in the Stroop task has found enhancement of task-relevant information and suppression of task-irrelevant information (Polk et al., 2008). These results are difficult to interpret as transient and sustained effects cannot be disentangled because of the use of a block design. Given the results of our study, only enhancement effects can be explained by trial-by-trial effects. The inhibitory effects then might be specific to the sustained configuration of the cognitive system, i.e., task-set implementation. If adaptation to recent conflict is implemented by strengthening the current task-set, then studies on task-set implementation should not show suppression of processing of task-irrelevant information. Therefore, the discrepancy of studies on task-set implementation and studies on adaptation to recent conflict suggests that the underlying mechanisms might differ.

It is important to note that in the PDP model cognitive control could be implemented in various ways: At the input level cognitive control could act by activation of units that process

task-relevant information, inhibition of units that process task-irrelevant information, or both. Furthermore, at the output level attention could modulate input signals of the response system by altering the connection weights between the input and output units or changing the output units' baseline activity (cp. Gratton et al., 1992), or a mixture of these mechanisms. While in the conflict adaptation model (Cohen et al., 1990) a task-set is implemented by enhancement of processing of task-relevant information, it is important to note that in other psychological models successful task performance in the Stroop task is often thought to result solely from suppression of task-irrelevant information. For instance, the greater Stroop effect in older adults (e.g., Logan, 1980; West and Alain, 2000; Langenecker et al., 2004) and in patients with schizophrenia (e.g., Henik et al., 2002; Henik and Salo, 2004) is proposed to result from a decline in the ability to inhibit processing of irrelevant sensory input (e.g., Cohn et al., 1984; Dulaney and Rogers, 1994). Similarly, deficits in inhibitory functions was proposed to underlie working memory impairment in the elderly (Gazzaley et al., 2005). Whether inhibition is one of the mechanisms of cognitive control is currently still highly debated. It is important to note that while we did not find evidence of suppression of early visual processing of task-irrelevant information, we cannot exclude that other areas involved in processing task-irrelevant information (e.g., higher-level language areas) have been suppressed.

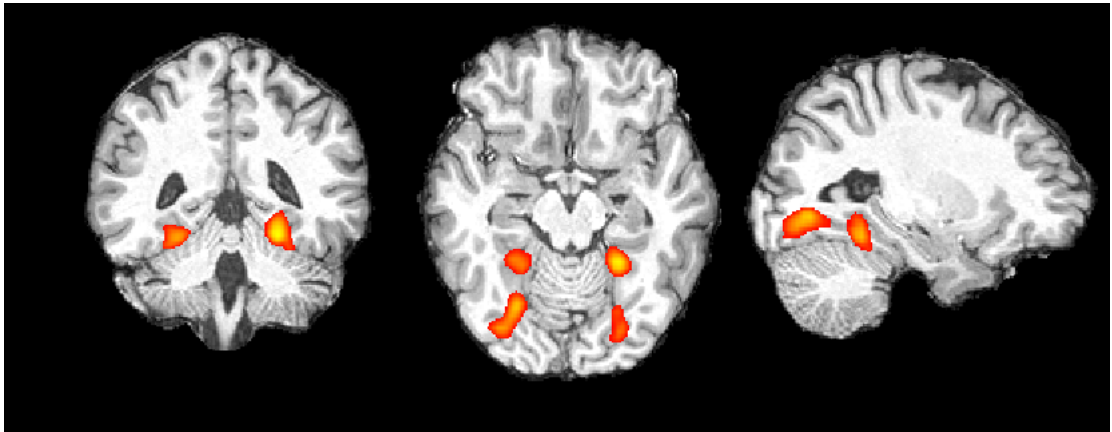


Figure 3.3: Single subject data, color vs. non-color blocks (for display purposes thresholded at $z > 6.0$; image presented in radiologic convention).

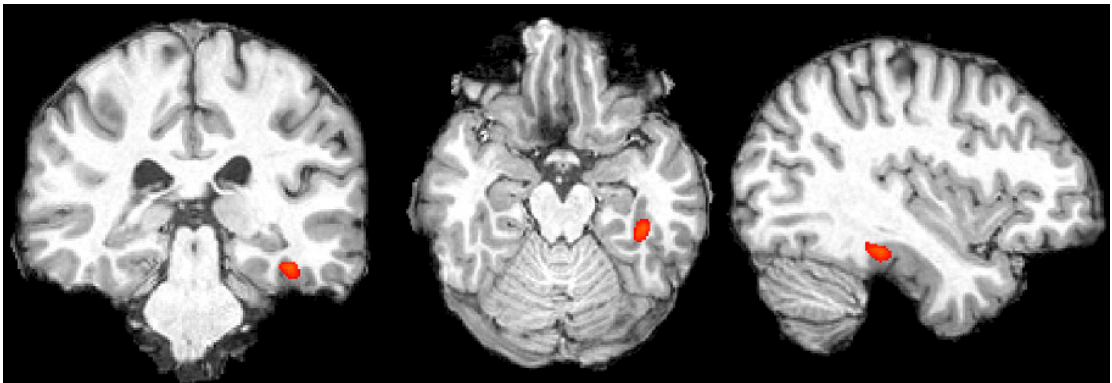


Figure 3.4: Single subject data, words vs. number blocks (for display purposes thresholded at $z > 6.0$; image presented in radiologic convention).

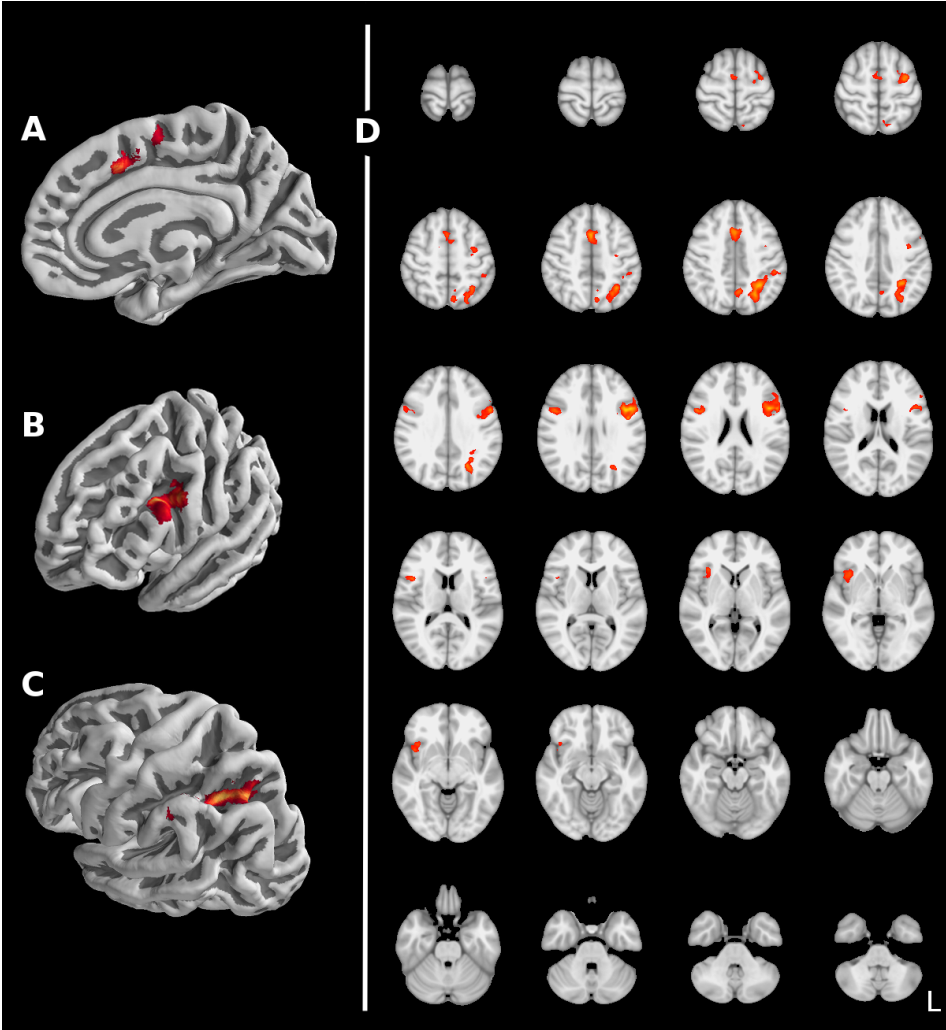


Figure 3.5: Stroop task: Incompatible vs. compatible trials ($z > 3.1$, $p < 0.05$ with clustersize $> 878 \text{ mm}^3$, (A) paracingulate gyrus, (B) inferior frontal junction, (C) superior parietal lobule, (D) axial slices).

4

The Effect of Trait Anxiety on Conflict Adaptation

The aforementioned theories (Botvinick, et al., 2001; Gratton et al., 1992) represent a unitary mechanism account of conflict adaptation. Although such an account is highly parsimonious, recent evidence suggests that adaptation to recent and adaptation to frequent conflict can be dissociated and might therefore rely on different neurocognitive mechanisms.

Models pointing to an important difference between adaptation to recent and adaptation to frequent conflict have been put forward recently. For instance, in the dual mechanisms of control theory (Braver, 2007, Braver, 2012) a proactive control mode is distinguished from a reactive control mode. It is argued that proactive control, i.e., a sustained maintenance of task goals, needs more cognitive resources than reactive control, which is triggered to refresh/reactivate task goals by certain stimuli.

Because anxious people show more ruminations and worries, which bind cognitive resources, it is also predicted by dual mechanisms of control theory that negative mood states and anxiety-related personality traits lead to stronger reliance on less demanding transient control processes. Therefore, anxious people should show stronger adaptation to recent conflict, but less pronounced adaptation to frequent conflict compared to less-anxious people.

Recent studies seem to support the first prediction. In these studies participants in whom an anxious or sad state was induced, showed increased conflict adaptation effects in a flanker task (van Steenbergen, Band, and Hommel, 2010). A later study replicated this effect and showed

Chapter 4. The Effect of Trait Anxiety on Conflict Adaptation

that the effect is not confined to a specific interference task or a specific mood induction procedure (Schuch and Koch, 2015). These authors interpret their findings with respect to conflict monitoring theory and argue that conflict monitoring is facilitated in anxious individuals, as in a sad or anxious state these individuals are biased towards negative events. Cognitive conflict might therefore become more salient or more aversive, leading to greater adaptation to recent conflict. Despite the different argumentation, their data are reconcilable with the dual mechanisms of control theory. Adaptation to frequent conflict was not examined in their studies.

That anxiety may improve a cognitive function is especially interesting, as anxiety is normally thought to be highly disruptive to everyday life. For instance, it is well established that anxious individuals show a bias for threat-related information (for a overview see Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, and van Ijzendoorn, 2007). There is also growing evidence for the negative impact of anxiety on attention and cognitive control in non-emotional contexts. Anxiety—both as personality dimension (i.e. trait anxiety) and as a transient mood state (i.e. state anxiety)—appears to impair performance, especially on attentionally demanding tasks (Derakshan and Eysenck, 2009). Attentional control theory (Eysenck et al., 2007), a prominent cognitive theory of anxiety, argues that individuals high in anxiety show impaired performance compared to individuals low in anxiety because high anxiety levels reduce the ability to process cognitive information efficiently. This deficit results mainly from highly anxious individuals having more irrelevant thoughts such as self-preoccupation and worry than less anxious individuals and coping with these thoughts affects performance negatively. Attentional control theory therefore predicts that anxious people show greater interference effects and less pronounced adaptation to recent and frequent conflict compared to less-anxious people.

With respect to interference and conflict adaptation effects, a recent study found neither an effect of trait anxiety on the interference effect nor on adaptation to recent conflict in a gender discrimination Stroop task (Osinsky, Alexander, Gebhard, and Hennig, 2010). Yet another study (Pacheco-Unguetti, Acosta, Callejas, Lupianez, 2010) found increased interference effects for participants high in trait anxiety in the attention network test (Fan, McCandliss, Sommer, Raz, and Posner, 2002) that assesses alerting, orienting, and executive control. Unfortunately, adaptation effects were not examined in this study. In sum, the results of studies concerning the influence of affect on interference and conflict adaptation in interference tasks are mixed so far.

In our study we examined if adaptation to recent and/or frequent conflict is affected by anxiety as a personality trait. We used the State-Trait Anxiety Inventory (STAI, Spielberger, et al., 1983) to measure anxiety in each participant. We then had participants perform a standard Stroop task, in which incompatible trials were presented with varying frequency in a block-wise fashion. During the first blocks compatible and incompatible trials were presented with equal probability. These blocks enabled us to examine adaptation to recent conflict. To control for episodic memory retrieval effects we used six different colors (and

color words) that were mapped onto six different response buttons. With this extended set of stimuli and responses it was possible to create a pseudorandom sequence without direct feature repetitions. During the last blocks compatible and incompatible trials were presented with differing probability. These blocks allowed us to examine adaptation to frequent conflict. The goal of the current study was twofold: Firstly, we wanted to examine the effects of trait anxiety on interference effects and adaptation to recent and frequent conflict. More explicitly, conflict adaptation theory predicts anxious participants to show stronger adaptation to recent and frequent conflict, whereas the dual mechanisms of control account predicts that anxious participants show stronger adaptation to recent conflict but less pronounced adaptation to frequent conflict, while attentional control theory predicts increased interference effects and less pronounced adaptation to recent and frequent conflict for anxious participants. Secondly, we wanted to examine if participants showing strong adaptation to recent conflict (devoid of feature repetition effects) also show strong adaptation to frequent conflict, as predicted by conflict adaptation theory but not dual mechanisms of control theory.

4.1 Methods

4.1.1 Participants

Seventy-five university students of the University of Magdeburg were recruited. Two participants had to be excluded because of technical problems. In the remaining group ($n=73$), age ranged from 19 to 43 years (median=23), forty-four participants were female, and twenty-nine were male. By self-report, all participants had normal or corrected to normal vision, were right handed, did not suffer from any psychiatric or neurological disorder and were naive with respect to the purpose of the study. All participated for partial course fulfillment and received a debriefing after the experiment. All procedures performed were in accordance with the declaration of Helsinki and its later amendments or comparable ethical standards (World Medical Association, 2013).

4.1.2 Apparatus and Stimuli

Participants performed a color word Stroop task (Stroop 1935). Six color words (blue, red, green, yellow, orange, violet) printed in different colors (blue, red, green, yellow, orange, violet) were presented at the center of the screen. Participants had to indicate the font color by pressing one of six response buttons. In compatible trials, print color and color word were the same. In incompatible trials, color and word differed. Colors were randomly assigned to response buttons for each participant. For ease of task performance the color button assignments were presented at the bottom part of the screen during the whole experiment. Compatible and incompatible trials were presented with a 50/50 ratio during the first four blocks and a 30/70 or 70/30 ratio during the last four blocks. During the session participants sat in a comfortable chair in a dimly lit room. A standard PC was used for stimulus presentation and recording

Chapter 4. The Effect of Trait Anxiety on Conflict Adaptation

responses. For responses, participants used their ring, middle and index fingers of their left and right hand on a response box with six response buttons (arranged in a row). Instructions and feedback were presented in white on a black background on a 24-inch TFT monitor. The distance to the computer screen was approximately 100 cm and size of the different stimuli ranged from 0.5° to 1.5° visual angle in the horizontal dimension. At the beginning participants filled out the state scale of the State-Trait-Anxiety-Inventory (Spielberger, et al., 1983). Participants were trained on the stimulus response mapping by responding to the color words printed in white with the left hand (30 trials), the right hand (30 trials) and both hands (30 trials). They were given 80 Stroop trials as training. Subsequently, they completed the eight experimental blocks. At the end of the experimental session the participants filled out both the state and the trait scale.

4.1.3 Procedure

For the Stroop task each trial comprised the following events: A blank screen was presented for 200ms, followed by a fixation cross at the center of the screen presented for 400ms, the color word stimulus presented for 300ms, and the presentation of a fixation cross for 1500ms. In case of an response error, an acoustic feedback was provided and the trial was repeated. In all other cases (correct response or no response), the next trial was presented. After a short training, participants performed eight blocks of approximately 100 trials each. After each block feedback for mean response time and error rate was provided. If more than 15% errors were committed, an additional instruction asking the participant to respond more cautiously or slowly was presented. If less than 5% error were committed, an additional instruction asking the participant to respond less cautiously and faster was presented. From our experience this procedure is effective in equalizing the cautiousness (speed-accuracy-trade-off) of participants. During the first four blocks compatible and incompatible trials were presented with 50/50 ratio of compatible to incompatible trials. For the last four blocks in two blocks compatible and incompatible trials were presented with a 30/70 ratio (high conflict condition) and with a 70/30 ratio (low conflict condition) in alternating order counterbalanced between participants. To control for episodic memory effects, stimulus sequences were pseudorandomized, such that neither the word nor the color in one trial would appear neither as word nor as color in the next trial.

4.1.4 Analysis

The first three trials were considered warm-up trials and excluded from the analyses. Also trials with missing responses were excluded from the analyses. Error rate was calculated as relative frequency of error trials from all remaining trials for each condition. Error trials and trials following an error were excluded from further analyses. Median response times and arcsine transformed error rates for correct trials were then subjected to separate analyses of covariance (ANCOVAs). For adaptation to recent conflict the following factors were included in the model: the within-subjects factors compatibility of the current trial (incompatible vs. compatible)

and compatibility of the previous trial (incompatible vs. compatible), and the between-subjects factor trait anxiety (low vs. high). To control for state anxiety normalized state anxiety scores were included as covariate. For adaptation to frequent conflict the following factors were included in the model: the within-subjects factors compatibility of the current trial (incompatible vs. Compatible) and conflict frequency (low vs. high), and the between-subjects factor trait anxiety (low vs. high). Again, normalized state anxiety scores were included as covariate. All statistical analyses were carried out using R (Version 3.2.0, R Development Core Team, 2015).

4.2 Results

4.2.1 Anxiety measures

STAI scores can range from 20 to 80. The mean state score was 35.8 (S.D.= 7.7, range = 22 to 58) before the experiment and 38.4 (S.D.= 7.5, range = 22 to 63) after the experiment ($t(72)=2.98$, $p < 0.01$). Pre- and post-experiment state anxiety scores were correlated ($r=0.50$, $t(71)=4.87$, $p < 0.001$). For the following analysis we averaged the pre- and post-experiment state anxiety scores, resulting in a mean score of 37 (S.D. = 6.6, range = 22 to 55). The mean trait score was 39 (S.D. = 9.7, range = 22 to 69). Trait and state anxiety scores were correlated ($r=0.57$, $t(71)=5.87$, $p<0.001$). We divided participants into two groups (high vs. low trait anxiety) by median split of the trait anxiety score.

4.2.2 Response Times and Error Rates

Recency Effect (first four blocks)

Participants responded more slowly to incompatible than compatible trials (978 ms vs. 868 ms; $F(1,70)=302.5$, $p<0.0001$; interference effect). This interference effect was reduced by 16ms after an incompatible trial (118 ms vs. 102 ms; $F(1,70)=8.5$, $p<0.01$; adaptation to recent conflict). Importantly, this adaptation effect was only seen in participants high in trait anxiety (reduction of 31 ms) but not in participants low in trait anxiety (reduction of 1 ms; $F(1,70)=6.2$, $p=0.01$; see Table 4.1). No other effects were significant (all $F<3.0$, all $p>0.09$).

Participants made more errors during incompatible trials (6.4% vs. 3.4%; $F(1,70)=70.5$, $p<0.0001$; interference effect). No other effects were significant.

Frequency Effect (last four blocks)

Participants responded more slowly to incompatible than compatible trials (926 ms vs. 812 ms; $F(1,70)=256.1$, $p<0.0001$; interference effect). This interference effect was reduced by 15 ms when incompatible trials were more frequent (108 ms vs. 123 ms; $F(1,67)=5.8$, $p<0.05$;

Chapter 4. The Effect of Trait Anxiety on Conflict Adaptation

Table 4.1: Response times (RT) and error rates (ER) showing a recency effect for anxious participants only.

trait anxiety	preceding trial	current trial			
		compatible		incompatible	
		RT	ER	RT	ER
low	compatible	877 (121)	3.1	980 (148)	5.6
	incompatible	873 (107)	3.5	975 (141)	6.4
high	compatible	857 (98)	3.0	990 (127)	7.2
	incompatible	867 (106)	4.1	969 (120)	6.3

Table 4.2: Response times (RT) and error rates (ER) showing a frequency effect for participants low and high in anxiety.

trait anxiety	conflict frequency	current trial			
		compatible		incompatible	
		RT	ER	RT	ER
low	25% incompatible	808 (107)	3.9	918 (141)	7.0
	75% incompatible	816 (100)	3.4	919 (140)	5.9
high	25% incompatible	809 (83)	4.2	943 (133)	6.8
	75% incompatible	813 (88)	4.0	927 (126)	6.5

frequency effect; see Table 4.2). All other effects were non-significant, especially there was no influence of trait anxiety on any of the measures.

Participants made more errors during incompatible trials (6.5% vs. 3.8%; $F(1,70)=34.9$, $p<0.0001$; interference effect). No other effects were significant.

4.3 Discussion

We examined the influence of trait anxiety on adaptation to recent and frequent conflict in the Stroop task. We tested hypotheses from two prominent cognitive control theories. Conflict adaptation theory (Botvinick et al., 2001) predicts greater adaptation to recent and frequent conflict, as conflict should be more aversive or salient for individuals high in trait anxiety. Dual mechanisms of control theory (Braver, 2007; Braver, 2012) predicts greater adaptation to recent and less pronounced adaptation to frequent conflict for individuals high in trait anxiety compared to individuals low in trait anxiety. According to this account, individuals high in trait anxiety should rely on less cognitive demanding control strategies, i.e. reactive

control, because ruminations and worries consume processing resources in these individuals. Finally, attentional control theory (Eysenck, Derakshan, Santos, and Calvo, 2007) predicts higher interference effects and possibly smaller conflict adaptation effects in highly anxious individuals.

Our main finding was that adaptation to recent conflict was seen in participants high in trait anxiety only, supporting the first hypothesis from conflict adaptation theory and dual mechanisms of control theory. Recent studies showed an effect of state anxiety on adaptation to recent conflict (van Steenbergen et al., 2010, Schuch and Koch, 2014). In these studies it was shown that individuals in whom a sad or anxious mood was induced showed greater adaptation to recent conflict. The authors explain their findings by pointing to the aversive nature of cognitive conflict and argue that this aversiveness drives conflict adaptation. Our results extend these findings by showing that anxiety as a personality trait (independent of state anxiety) seems to be relevant for conflict adaptation too. The influences of trait anxiety are often thought to be mediated by state anxiety and participants in our study that scored high on trait anxiety scored also higher on state anxiety. One might speculate that a bias for threat-related information (such as response conflict) brought individuals high in trait anxiety more often into an anxious state than individuals low in trait anxiety during the task. This increased state anxiety then resulted in increased adaptation to recent conflict. Nevertheless, as we controlled for state anxiety in our statistical analyses, our results implicate an independent influence of trait anxiety on conflict adaptation. Interestingly, a double dissociation between state and trait anxiety was previously found (Pacheco-Unguetti, et al., 2010). While high trait anxiety was related to deficiencies in the executive control network, state anxiety was related to an exaggerated activation of the orienting and alerting networks. In light of this study we favor the interpretation that trait anxiety has a genuine effect on conflict adaptation independent of state anxiety. It is important to note, that independent of the exact mechanisms by which trait anxiety influences conflict adaptation, our results have implications for any study of conflict adaptation. Our data show that trait anxiety might be an important variable influencing cognitive control. Therefore this variable should be controlled in studies examining cognitive control. All anxiety scores in our study were in the range of a normal population. That some studies found a conflict adaptation effect (e.g., Akçay and Hazeltine, 2008, Kerns et al., 2004, Purmann et al., 2009), while others did not (e.g., Fernandez-Duque and Knight, 2008, Wendt, et al., 2007) might have resulted from different proportions of low and high anxious participants in their studied samples.

Individuals high in trait anxiety did not differ from individuals low in trait anxiety in adaptation to frequent conflict. Conflict monitoring theory predicts greater adaptation to frequent conflict, as this effect stems directly from adaptation to recent conflict. Dual mechanisms of control theory predicts less pronounced adaptation to frequent conflict for trait-anxious individuals. According to this account, because of their occupation by ruminations and worries these individuals do not have enough resources for using proactive control strategies. In contrast to conflict adaptation theory our results suggest that adaptation to recent and adaptation to frequent conflict rely on different neurocognitive mechanisms. Nevertheless,

prediction from dual mechanisms of control theory could not be confirmed either. It could be argued that adaptation to frequent conflict was not measured unconfounded by adaptation to recent conflict. Participants might have—additionally to adaptation to frequent conflict—shown adaptation to recent conflict in the last blocks of the experiment. As individuals high in trait anxiety showed increased adaptation to recent conflict, this might have led to an overestimation of adaptation to frequent conflict in these individuals, and hence masked possible less pronounced adaptation to frequent conflict as predicted by dual mechanisms of control theory. To date no experimental procedure has been shown to robustly deconfound adaptation to frequent conflict from adaptation to recent conflict. We know of only one study that was able to deconfound adaptation to frequent conflict from adaptation to recent conflict (Mayr and Awh, 2009). In this study adaptation to recent conflict was seen in the first two task blocks but not in the last two blocks while adaptation to frequent conflict was seen throughout the experiment. Importantly, individuals low in trait anxiety showed adaptation to frequent conflict without showing adaptation to recent conflict. Our data can best be explained by the idea of greater aversiveness of conflict for anxious individuals (van Steenbergen et al., 2010, Schuch and Koch, 2014). Anxious individuals show greater adaptation to recent conflict because conflict is more aversive in these individuals and hence lead to stronger recruitment of control mechanisms. On the other hand, they show the same level of adaptation to frequent conflict as individuals low in anxiety, as here due to the repeated exposure to conflict control mechanisms are maximally engaged and control capabilities to not differ between both groups of individuals.

More pronounced adaptation to recent conflict for participants high in trait anxiety is highly interesting, as anxiety is normally thought to be highly disruptive to everyday life. While it is well established that anxious individuals show a bias for threat-related information (for a review see Bar-Haim, et al., 2007), there is also growing evidence for the impact of anxiety on attention and cognitive control in non-emotional contexts. Neurocognitive deficits in cognitive control and response monitoring in patients with anxiety disorders (such as OCD) have been established already (Kim, Kim, Yoo, and Kwon, 2007, Ursu, Stenger, Shear, Jones, and Carter, 2003). Subclinical anxiety – that is anxiety both as personality dimension (i.e. trait anxiety) and as a transient mood state (i.e. state anxiety) – also seems to impair performance, especially on attentionally demanding tasks (for a review see Eysenck and Calvo, 1992). Attentional control theory (Eysenck et al., 2007) predicts higher interference effects and possibly smaller conflict adaptation effects in highly anxious individuals. In our study individuals high and low in trait anxiety showed interference effects of equal size with greater adaptation to recent conflict in individuals high in trait anxiety. Nevertheless, attentional control theory further states that both effects might be counteracted by compensatory mechanisms. In attentional control theory it is further argued that negative effects might not be seen at the behavioral level, because deficits can be compensated by increased effort. Therefore, highly anxious people are less efficient but might be equally effective than less anxious people. Support for this efficiency hypothesis comes from neuroimaging studies that show comparable behavioral performance but increased activation of brain areas related to cognitive control for anxious people (e.g.

Basten, Stelzel, and Fiebach, 2011). The absence of higher interference effects for high trait anxious participants is therefore reconcilable with this theory. Nevertheless, improved performance (i.e. greater adaptation to recent conflict) in these individuals is difficult to explain for attentional control theory. Interestingly, better task performance for individuals high in trait anxiety has been found in a number of studies. For instance, Sehlmeier and colleagues found decreased false alarm rates in a NoGo-task for individuals high in trait anxiety while there was no difference in response times for individuals high and low in trait anxiety (Sehlmeier, et al., 2010). Together with an increased amplitude of the NoGo-N2 ERP component they interpreted their results as enhanced response inhibition in individuals high in trait anxiety.

The comparable size of interference effects in both groups is also important for the interpretation of results. We recently found that adaptation to recent conflict depends on the size of interference in the previous trial (Wendt, et al., 2014). Therefore, more pronounced adaptation to recent conflict for individuals high in trait anxiety could be attributed to the increased interference in this group. As in our study the two groups did not differ with respect to the size of the interference effect we can rule out this alternative explanation.

To summarize: We found adaptation to recent conflict only in individuals high in trait anxiety, but adaptation to frequent conflict in individuals both high and low in anxiety. We interpret these results as evidence that both behavioral effects are based on different neurocognitive mechanisms. Our data fit best the idea of increased aversiveness of conflict in anxious individuals. Furthermore, the results suggest that future studies of conflict adaptation should control for trait anxiety.

5

Tight Control of Stimulus Sequence and Frequency of Individual Stimuli

A recent study was able to deconfound adaptation to frequent conflict from adaptation to recent conflict (Mayr and Awh, 2009). In this study participants performed a Stroop task with varying conflict frequencies in different task blocks. Adaptation to recent conflict was evident in the first two blocks of the experiment only. In contrast, adaptation to frequent conflict was found over the whole course of the experiment. This result is theoretical importance, as prominent theories of cognitive control assume that adaptation to recent and adaptation to frequent conflict are based on the same mechanism (Gratton et al., 1992, Botvinick, et al., 2001).

Nevertheless, practice and contingency effects due to overall more frequent presentation of individual stimuli have not been controlled in this study. It has been argued, that, because practice effects for specific stimulus ensembles and stimulus-response contingencies, more frequent presentation of specific stimuli leads to a processing advantage for these stimuli (Mordkoff, 1996, Wendt and Luna-Rodriguez, 2009). For instance, when using red and blue as stimuli in a Stroop task, in blocks with 75% incompatible trials the word RED in blue and the word BLUE in red are presented three times as often as the word RED in red and word BLUE in blue. This by itself might give incompatible stimuli a processing advantage. Furthermore, the word RED in blue is more often followed by the word RED in blue than the word BLUE in blue is by the word BLUE in blue. The word BLUE in red is followed more often by the word BLUE in red than the word RED in red is followed by the word RED in red. This might give incompatible stimuli a processing advantage because of stimulus and response priming.

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It is normally assumed that the task-irrelevant stimulus does not contain any information with respect to the response to be given. But with 75% incompatible trials when red occurs as word red is the correct response in most trials. Likewise, when blue occurs as word blue is the correct response in most trials. In other words, under conditions of an unequal number of presentations of incompatible and compatible trials, the task-irrelevant information actually contains information.

It has to be noted that these ideas are especially relevant for adaptation to frequent conflict. Also, as frequency of the presentation of individual stimuli is often not controlled, frequency of individual stimulus ensembles or stimulus-response contingencies cannot be ruled out as explanation for adaptation to frequent conflict like patterns in response times in most studies. Nevertheless, if more than two stimuli and responses are used—for instance when controlling for sequences of stimulus features—this confound also develops for adaptation to recent conflict. Unfortunately, so far there is no simple method to create stimulus sequences devoid of such confounds.

In the study mentioned above (Mayr and Awh, 2009) it is therefore possible that the adaptation to frequent conflict observed resulted—at least in part—from these non-attentional effects and not from increased selectivity of information processing. The conclusion that adaptation to recent conflict and adaptation to frequent conflict are based on different mechanisms might therefore not be warranted, as the disappearance of adaptation to frequent conflict might have been masked by these effects.

In this experiment we strived to replicate the results of Mayr and Awh (2009) while avoiding the aforementioned confounds. We had participants perform a Stroop-like task. In the first four and last four blocks compatible and incompatible trials were presented with equal frequency. These blocks were used to examine adaptation to recent conflict early and late in the experimental session. In-between we presented eight blocks with alternating high or low frequency of incompatible trials. These blocks were used to examine adaptation to frequent conflict. As in the other Stroop experiments reported in this thesis, stimulus sequence was controlled in that the word in one trial was never used as word or color in the next trial and the color in one trial was never used as word or color in the next trial. Additionally, we controlled the overall frequency of a subset of stimuli. To this end four specific stimuli, two compatible and two incompatible were presented five times per block. The remaining stimuli were used to create defined proportions of incompatible trials per block.

5.1 Methods

5.1.1 Participants

Seventeen students of the University of Magdeburg were recruited. One participant had to be excluded because he was not able to learn the stimulus response mapping with the training provided. In the remaining group (n=16), age ranged from 21 to 31 years (median=25), 12

participants were female. By self-report, all participants had normal or corrected to normal vision, were right handed, did not suffer from any psychiatric or neurological disorder and were naive with respect to the purpose of the study. All participated for partial course fulfillment and received a debriefing after the experiment. All procedures performed were in accordance with the declaration of Helsinki and its later amendments or comparable ethical standards (World Medical Association, 2013).

5.1.2 Apparatus and Stimuli

Participants performed a color word Stroop task (Stroop 1935). Six color words (blue, red, green, yellow, orange, violet) printed in different colors (blue, red, green, yellow, orange, violet) were presented at the center of the screen. Participants had to indicate the font color by pressing one of six response buttons. In compatible trials, print color and color word were the same. In incompatible trials, color and word differed. Participants were trained on the stimulus response mapping by responding to the color words printed in white with the left hand (30 trials), the right hand (30 trials) and both hands (30 trials). Subsequently, participants completed one block of 96 trials of the Stroop task as training and 16 experimental blocks of 80-100 trials each (see below). Compatible and incompatible trials were presented with a 50/50 ratio during the first four and last four blocks of the experiment. A 30/70 or 70/30 ratio were presented during the middle eight blocks with the high conflict and low conflict condition presented in alternating order counterbalanced between participants. The four trials at the beginning of the block were all incompatible in blocks with high frequency of incompatible trials and all compatible in blocks with high frequency of compatible trials. To increase the interference effect, participants were trained again on the stimulus response mapping for twelve trials with both hands between experimental blocks. Participants hence had to respond to the word meaning in these training blocks. Switching between word naming and color naming is known to increase interference for color naming in following trials (Allport et al., 1994; Allport and Wylie, 1999).

During the session participants sat in a comfortable chair in a dimly lit sound attenuated room. Psychopy running on a standard PC was used for stimulus presentation and recording responses. For responses, participants used their ring, middle and index fingers of their left and right hand on the y, x, c, b, n, and m keys on a standard USB keyboard. Instructions and feedback were presented in white on a grey background on a 24-inch TFT monitor. The distance to the computer screen was approximately 100 cm and size of the different stimuli ranged from 0.5° to 1.5° visual angle in the horizontal dimension.

5.1.3 Procedure

A path finding algorithm was used to create four sets of pseudo-random stimulus sequences. Complete permutation of colors and words results in 36 different stimuli of which six are compatible and 30 are incompatible. To control for confounding non-attentional effects

caused by more frequent presentation of certain individual stimuli, we controlled the frequency of a subset of stimuli while the frequency of the rest of stimuli was allowed to vary. More specifically, the word RED in red, the word RED in blue, the word GREEN in green and the word GREEN in yellow were each presented five times per block. The rest of the stimuli was used as fill-up stimuli to create the ratio of incompatible to compatible trials required for the three block conditions (50/50, 30/70, 70/30). To rule out episodic memory retrieval, neither the color nor the word was repeated from one trial to the next and the color of one trial was never used as the word in the next trial and the word of one trial was never used as color in the next trial. To this end we developed an algorithm, which uses a look-up table for allowed stimulus to stimulus transitions. For the generation of a sequence the twenty test stimuli were placed at random positions in this sequence always separated by one to six fill-up stimuli. Then a fill-up stimulus was chosen as start stimulus and the next stimulus was chosen based on the allowed stimulus to stimulus transitions. Tables for the frequency of each stimulus and for the frequency of stimulus to stimulus transitions used in the sequence so far provided another constraint, avoiding extremely unbalanced stimulus sequences. In the case there is no allowed transition from a fill-up stimulus to the next test stimulus, the algorithm goes back two positions in the sequence and continues with another fill-up stimulus.

For the Stroop task each trial comprised the following events: A fixation cross was presented at the center of the screen for 400ms, the color word stimulus presented for 300ms, and then the fixation cross was presented till a response was given. No error feedback was provided. After each block participants were allowed to have a break and continue with the next block at a self-determined point in time.

5.1.4 Analysis

For each block only the ten compatible and ten incompatible trials for which the presentation frequency was controlled were used in subsequent analyses. Trials following an error were excluded from further analyses. Error rate was calculated as relative frequency of error trials from the remaining trials for each condition. Error trials were then excluded from further analyses and median response times were calculated for each subject and condition. Arcsine transformed error rates and response times were subjected to two separate analyses of variance (ANOVAs). For adaptation to recent conflict the following factors were included in the model: the within-subjects factors compatibility of the current trial (incompatible vs. compatible) and compatibility of the preceding trial (incompatible vs. compatible). For adaptation to frequent conflict the following factors were included in the model: the within-subjects factors compatibility of the current trial (incompatible vs. Compatible) and conflict frequency (low vs. high). To test if participants showing stronger adaptation to recent conflict also show stronger adaptation to frequent conflict we conducted a t-test. All statistical analyses were carried out using R (Version 3.2.0, R Development Core Team, 2015).

Table 5.1: Recency effect in Experiment 4: Response times (and standard deviation) in ms and error rates in percent.

phase	preceding trial	current trial			
		compatible		incompatible	
		RT	ER	RT	ER
early	compatible	759 (76)	1.7	790 (70)	1.6
	incompatible	725 (94)	4.7	847 (151)	5.1
late	compatible	710 (69)	2.1	757 (82)	2.4
	incompatible	718 (68)	9.7	766 (80)	3.5

5.2 Results

5.2.1 Response Times and Error Rates

Recency Effect (blocks 1-4 and 13-16)

Overall, participants responded more slowly during the first compared to the last four blocks (780 ms vs. 743 ms; $F(1,15)=9.7$; $p<0.01$). They furthermore responded more slowly to incompatible than compatible trials (793 ms vs. 731 ms; $F(1,15)=41.3$, $p<0.0001$; interference effect). Overall, this interference effect was not modulated by conflict in the preceding trial ($F(1,15)=4.5$; $p=0.052$). Nevertheless, there was a three-way interaction between time (block 1-4 vs. block 13-16), conflict level of the preceding trial and conflict level of the current trial ($F(1,15)=6.0$; $p<0.03$). No other effect was significant. Separate ANOVAs for the first four and last four blocks were run. During the first four blocks participants responded more slowly to incompatible than compatible trials (818 ms vs. 742 ms; $F(1,15)=18.6$, $p<0.001$; interference effect). Furthermore, this interference effect was modulated by conflict in the preceding trial ($F(1,15)=7.0$; $p<0.02$), but in an unexpected way: Interference was greater after an incompatible trial (122ms vs. 31ms). There was no main effect of conflict in the preceding trial. During the last four blocks participants responded more slowly to incompatible than compatible trials (762 ms vs. 714 ms; $F(1,15)=12.3$, $p<0.01$; interference effect). No other effect was significant.

Overall, error rates were 3.8%, and for the first four and last four blocks together error rates were greater after an incompatible trial (5.5% vs. 1.9%; $F(1,15)=18.9$, $p<0.001$). No other effect was significant.

Frequency Effect (blocks 5-12)

Overall, participants responded more slowly to incompatible than compatible trials (778 ms vs. 728 ms; $F(1,15)=14.9$, $p<0.002$; interference effect). This interference effect was modulated

Chapter 5. Tight Control of Stimulus Sequence and Frequency of Individual Stimuli

Table 5.2: Frequency effect in Experiment 4: Response times (and standard deviation) in ms and error rates in percent.

conflict frequency	compatible		incompatible	
	RT	ER	RT	ER
25% incompatible	718 (65)	4.1	787 (100)	5.5
75% incompatible	738 (76)	5.7	769 (88)	12.7

by conflict frequency ($F(1,15)=8.3$, $p<0.02$; frequency effect) with an interference effect of 31 ms when incompatible trials were more frequent and an interference effect of 69 ms when incompatible trials were infrequent. There was no main effect of conflict frequency.

Participants made more errors during incompatible trials than during compatible trials (8.8% vs. 4.9%; $F(1,15)=8.1$, $p=0.012$; interference effect). Participants made also more errors when incompatible trials were more frequent (8.9% vs. 4.8%; $F(1,15)=17.0$, $p<0.001$). Furthermore, there was an interaction of compatibility level of the current trial and conflict frequency ($F(1,15)=5.6$, $p=0.03$). The difference in error rate between compatible and incompatible trials was greater, when incompatible trials were more frequent (7% vs. 1.4%).

5.3 Discussion

We examined adaptation to recent and adaptation to frequent conflict while controlling for stimulus-sequence effects and overall frequency of individual stimuli. The need for rigorous control of stimulus sequence and stimulus frequency when examining adaptation to recent and adaptation to frequent conflict has been recognized (Duthoo et al., 2014), but is often neglected. It is not trivial to generate stimulus sequences by which attentional and non-attentional mechanisms of modulation of interference effects can be deconfounded. In this study we used a path finding algorithm to create such a stimulus sequence.

Our main finding was a reverse adaptation to recent conflict effect, i.e., greater interference after incompatible trials, that has disappeared at the end of the experiment, whereas there was robust adaptation to frequent conflict. While this effect is difficult to explain, it seems to be robust: Twelve out of 16 participants showed this effect. Interestingly, reversed adaptation to recent conflict has been found in other recent studies (Notebaert and Verguts, 2008, Braem, Verguts, and Notebaert, 2011). A reversed conflict adaptation effect was seen when switching between tasks and this switch lead either to a change in the task-relevant information (orientation vs. color) or of the effector (hand vs. foot). One could speculate that because of the experimental control of the presentation frequency of our test stimuli these stimuli might have gained the character of a separate task.

Nevertheless, the main purpose of the study was to test the hypothesis that adaptation to recent and adaptation to frequent conflict are based on different mechanisms. We can state that the results are clearly not compatible with the notion of a one-fits-all mechanism of conflict adaptation. In this respect we were able to replicated the results of Mayr and Awh (2009).

6

Summary and General Conclusion

For successful behavior, information processing has to be selective and selectivity of information processing has to be continuously fine-tuned in response to changing situational demands. In interference tasks reduced interference has been found under conditions of recent and frequent conflict (Gratton, et al., 1992, Logan and Zbrodoff, 1979), Kerns et al., 2004), reflecting such fine-tuning. Whereas current theories such as the conflict monitoring theory (Botvinick, et al., 2001) assume the same attentional mechanism underlying both effects, recent evidence raises doubts on this notion.

In a study using the flanker task the overall frequency of compatible and incompatible stimuli was varied between two groups of participants and a dissociation between both adaptation effects was found (Purmann, et al., 2009). In this study response times were decomposed into movement initiation times and movement execution times. Whereas adaptation to frequent conflict was evident in movement initiation and execution times, adaptation to recent conflict was confined to movement execution times. Another study (Mayr and Awh, 2009) used a Stroop task and found adaptation to recent conflict in the first two blocks of the experiment only. In contrast, adaptation to frequent conflict was found over the whole course of the experiment. Another study used two different interference tasks to test if adaptation effects transfer from one task to the other (Fernandez-Duque and Knight, 2008) and found both – adaptation to recent and adaptation to frequent conflict – to be task-specific. Nevertheless, adaptation to recent conflict in this study could be fully explained by episodic memory retrieval effect (see below) while adaptation to frequent conflict was still present after controlling for these effects. Another series of studies examined the task specificity of conflict adaptation processes. In one study trials of a spatial Stroop task and a Simon task were presented in random order (Funes,

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et al., 2010). They found only adaptation to frequent conflict to be task-general. Adaptation to recent conflict did not generalize to the other task. In a follow-up study one group of subjects worked on two blocks of trials of the Simon task with a 75/25 ratio of compatible trials to incompatible trials, while another group worked on two blocks of trials of the Simon task with 25/75 ratio of compatible trials to incompatible trials (Torres-Quesada, et al., 2013). In the following blocks trials of a flanker task were intermixed within trials of the Simon task. It was found that adaptation to recent conflict was task-specific, but adaptation to frequent conflict generalized to the other task. Furthermore, adaptation to frequent conflict was found to be a sustained effect, as it could still be observed in the first two post-training blocks with a 50/50 ratio of compatible to incompatible trials.

In four experiments we further tested the hypothesis that adaptation to recent and adaptation to frequent conflict are based on different underlying mechanisms.

A recent ERP study found that early visual ERP components were modulated by conflict in the preceding trial. In an ERP study we found interference effects in N2 and P3 and modulation thereof by frequent conflict. Nevertheless, early visual ERP components were not modulated by frequent conflict, suggesting that adaptation to frequent conflict involves modulation of later cognitive processes, and in this respect is different from adaptation to recent conflict, which involves modulation of early sensory processes.

That adaptation to recent conflict involves facilitation of processing of task-relevant information has been suggested by an fMRI study using a face-word Stroop task (Egner and Hirsch, 2005). Increased activation in the fusiform face area has been found for incompatible trials following an incompatible trial, but only when faces were the task-relevant stimulus. No modulation by compatibility level of the preceding trial was found when the words/names were the task-relevant stimulus. This result is interesting, as a related fMRI study on task-set implementation in the Stroop task has found enhancement of task-relevant information and suppression of task-relevant information (Polk et al., 2008). In this study participants had to perform blocks of a Stroop task, with all stimuli being incompatible in some blocks and neutral in other blocks. For incompatible compared to neutral Stroop blocks they found increased activity in V4 and decreased activity in the VWFA. The authors concluded that both facilitation of processing of color information and suppression of processing of word information is part of task-set implementation. Conflict monitoring theory uses only one mechanism—facilitation of processing of the relevant information—for task-set implementation, adaptation to recent conflict and adaptation to frequent conflict. The results of these two studies suggest different mechanisms for task-set implementation and adaptation to recent conflict.

Importantly though, both studies have to be interpreted carefully. The first study uses a face-word Stroop task which—in contrast to the color-word Stroop task—uses non-integrated stimuli. Interference effects in Stroop-like tasks with non-integrated stimuli have been shown to be smaller (MacLeod, 1991), suggesting differences in the underlying mechanisms. If effects found in the face-word Stroop task generalizes to the color-word Stroop task (and vice versa)

is currently not known. Furthermore, in the experimental design they used, participants had to switch between face discrimination and word discrimination in a block-wise fashion. This manipulation was necessary to be able to examine activity in the FFA under two conditions, when faces were task-relevant and task-irrelevant, respectively. It is known that switching between two task-sets in a block-wise fashion can lead to carry-over effects from one block to another (Allport et al., 1994; Allport and Wylie, 1999; Monsell, 2003). The presence of task-set inertia is reflected in the observation that participants in this study showed interference effects under both task-sets, while normally Stroop interference is asymmetric. Nevertheless, how task-set inertia effects interact with conflict adaptation effects is currently not well understood. In the second study transient and sustained effects cannot be separated because of the use of a block design. The observed facilitation and inhibition effects can therefore reflect task-set implementation, adaptation to recent conflict, and/or adaptation to frequent conflict.

In an fMRI experiment we tried to further clarify the neural mechanisms underlying adaptation to recent conflict. We had participants perform a color-word Stroop task. In the same session participants performed two other tasks that were used to localize V4 and the VWFA. We observed increased activity in V4 for incompatible trials following incompatible trials while activity in the VWFA was not modulated by conflict level in the preceding trial. We thereby replicated the results from the face-word Stroop task (Egner and Hirsch, 2005). We conclude that adaptation to recent conflict in Stroop-like tasks (color-word Stroop task, face-word Stroop task) seems to mainly involve enhancement of task-relevant information but not suppression of task-irrelevant information and that this mechanism differs from the mechanisms underlying other instances of cognitive control, such as task-set implementation and adaptation to frequent conflict. Furthermore, as modulation of early visual information processing was restricted to incompatible trials following incompatible trials—and this is true for the three studies on adaptation to recent conflict (Egner and Hirsch, 2005, Scerif, et al., 2006, Purmann and Pollmann, 2014)—the idea of the conflict adaptation model that adaptation to recent conflict is based on facilitation of task-relevant information processing after conflict trials is too simple. In that case one would expect to find increased activity also for compatible trials after an incompatible trial. The model in its current form cannot explain the interaction of compatibility level of the current and the preceding trial.

Models pointing to an important difference between adaptation to recent and adaptation to frequent conflict have been put forward recently. For instance, in the dual mechanisms of control theory (Braver, 2007; Braver, 2012) a proactive control mode is distinguished from a reactive control mode. It is argued that proactive control, i.e. sustained maintenance of task goals, needs more cognitive resources than reactive control, which is triggered to refresh/reactivate task goals by certain stimuli. Transferred to interference tasks and adaptation to recent and adaptation to frequent conflict two control mechanisms seem possible in which one mechanism enforces a task-set (strategic adaptation to frequent conflict), whereas the other responds to changes in the need for cognitive control on a trial-by-trial basis (adaptation to recent conflict). This idea is comparable to the notion of micro- and macro-adjustments (Ridderinkhof, 2002).

Chapter 6. Summary and General Conclusion

One important hypothesis derived from dual mechanisms of control theory is that anxious people rely more on less demanding reactive control mechanisms than on more demanding proactive control mechanisms, because anxious people are occupied more by ruminations and worrying, which consumes attentional resources. We tested this hypothesis in a behavioral experiment by using a Stroop-like task and manipulated conflict frequency between blocks. Participants were divided into two groups based on their scores in the state-trait anxiety inventory (Spielberger, et al., 1983). We found adaptation to recent conflict in the high anxious group only whereas both groups showed equal adaptation to frequent conflict. Although these results do not fit dual mechanisms of control theory without further assumptions, the results suggest that adaptation to recent and adaptation to frequent conflict are based on different cognitive mechanisms.

In the last experiment we tried to replicate a recent study that found a simple dissociation between adaptation to recent and adaptation to frequent conflict (Mayr and Awh, 2009). In contrast to this study, we controlled the frequency of presentation for a subset of stimuli to rule out practice effects for specific stimulus ensembles and effects of stimulus-response contingencies (Mordkoff, 1996, Wendt and Luna-Rodriguez, 2009). Participants performed a Stroop task and we manipulated the frequency of incompatible trials per block (50% in the first four and last four blocks, and alternating 70% and 30% in the middle eight blocks). A subset of incompatible and compatible trials was presented a fixed number of times and only this subset was used to test adaptation to recent and adaptation to frequent conflict effects. We found that modulation of the interference effect by recent conflict was confined to the beginning of the experiment (replicating Mayr and Awh, 2009). Nevertheless, in contrast to most studies Stroop interference in our study was higher after an incompatible trial. Most importantly, we found (normal) adaptation to frequent conflict, that can not explained by a reversed (or absent; last four blocks of the experiment) adaptation to recent conflict effect.

Considering the evidence provided by the other studies reported above and the evidence provided by the experiments presented in this thesis it seems more and more unlikely, that adaptation to recent and adaptation to frequent conflict are based on the same underlying mechanism.

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--- Dies ist ein Muster ---

Erklärung

Hiermit erkläre ich, dass ich die von mir eingereichte Dissertation zum dem Thema

Different Mechanisms Underlying
Adaptation to Frequent and Adaptation to Recent Conflict

selbständig verfasst, nicht schon als Dissertation verwendet habe und die benutzten Hilfsmittel und Quellen vollständig angegeben wurden.

Hiermit erkläre ich, dass ich diese Arbeit nicht schon als Dissertation zur Erwerbung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.) an anderen Einrichtungen eingereicht habe.

oder
entsprechend abändern

Magdeburg, den 26.04.16

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