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Temporal and task-specific profiles of effort investment

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Summary

Investment of cognitive effort plays an important role in many aspects of daily life. For example, it can lead to feelings of cognitive fatigue, it is perceived as aversive and therefore avoided if possible, and it is registered as a cost in decision making. Cognitive effort can be invested through the application of cognitive control, which entails a flexible adjustment of behavior to environmental demands. For example, when faced with conflicting response options, we need to adaptively allocate cognitive control to overcome automatic response tendencies in favor of more appropriate behavior. Because cognitive control is effortful, it requires a balance between exerting a sufficient amount (to solve hard tasks), but not too much (to spare costly cognitive effort). This suggests that that cognitive control is best applied at variable time scales: transiently when conflict is rare but in a sustained way when conflict is frequent. In chapter 2, a behavioral quantification of this time scale is introduced. The chapter shows that cognitive control is indeed applied on a short time scale when conflict is rare or the context is volatile, and on a longer time scale when conflict is more frequent. The fMRI study in chapter 3 elaborates on these findings and shows that time scale differences are also mirrored in the neural implication of cognitive control. Increased transient activity was found in fronto-parietal areas when cognitive control was required rarely, while sustained neural activity was found in similar regions when cognitive control was required frequently. These results illuminate how context-dependent transient and sustained control subtend the same brain areas but operate on different time scales. Whereas chapters 2 and 3 deal with the temporal dynamics of cognitive effort through allocation of cognitive control (i.e., they expose *when* cognitive effort is applied), chapter 4 focuses on *how* effort investment is implemented neurally. The fMRI study in this chapter shows increased connectivity between dorsal anterior cingulate cortex (dACC) and task-specific cortical areas when effort demand is high. This implies that dACC, together with anterior insula and intraparietal sulcus, constitutes a general effort-responsive circuitry, and that dACC connects to specialized lower-level brain regions, depending on task specifics. Taken together, these studies provide 1) a behavioral and 2) a neural signature of temporal variations in the allocation of effortful control, and 3) show that the neural implementation of cognitive effort involves dACC-initiated sensitization of task-dependent areas.

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Samenvatting

Het leveren van cognitieve inspanning speelt een belangrijke rol in veel aspecten van het dagelijks leven. Cognitieve inspanning kan bijvoorbeeld leiden tot cognitieve vermoeidheid, wordt als aversief ervaren en daarom indien mogelijk vermeden, en is kostbaar, waardoor het invloed heeft op het nemen van beslissingen. Cognitieve inspanning kan geleverd worden door het toepassen van cognitieve controle, wat inhoudt dat gedrag op flexibele wijze wordt aangepast aan de veranderende vereisten van de omgeving. Wanneer we geconfronteerd worden met conflicterende responsopties, bijvoorbeeld, moeten we adaptieve cognitieve controle uitoefenen om automatische reacties te inhiberen ten gunste van beter passende acties. Omdat cognitieve controle kostbaar is, moet het op een efficiënte manier toegepast worden. Er moet genoeg controle toegepast worden om moeilijke taken op te lossen, maar niet teveel om de cognitieve inspanning niet te groot te maken. Dit suggereert dat cognitieve controle het best kan worden toegepast op variabele tijdschalen: kortstondig wanneer conflict niet vaak voorkomt, maar op een aanhoudende manier wanneer conflict frequent voorkomt. In hoofdstuk 2 wordt een gedragsmatige kwantificatie van deze tijdschaal geïntroduceerd. Dit hoofdstuk toont aan dat cognitieve controle inderdaad wordt toegepast op een korte tijdschaal wanneer conflict zeldzaam is of de context volatiel, en op een langere tijdschaal wanneer conflict vaker voorkomt. De fMRI-studie in hoofdstuk 3 gaat dieper in op deze bevindingen en laat zien dat verschillen in tijdschaal ook worden weerspiegeld in de neurale implicatie van cognitieve controle. Verhoogde kortstondige activiteit werd gevonden in fronto-pariëtale hersenregio's wanneer cognitieve controle maar af en toe nodig was, terwijl aanhoudende neurale activiteit werd gevonden in vergelijkbare regio's wanneer cognitieve controle vaak nodig was. Deze resultaten laten zien dezelfde hersengebieden betrokken zijn bij kortstondige en aanhoudende controle, maar op verschillende tijdschalen actief zijn. Terwijl hoofdstuk 2 en 3 handelen over de temporele dynamiek van cognitieve inspanning door uitoefening van cognitieve controle (d.w.z. over de vraag *wanneer* cognitieve inspanning wordt toegepast), richt hoofdstuk 4 zich op hoe cognitieve inspanning neuraal wordt geïmplementeerd. De fMRI-studie in dit laatste hoofdstuk laat een verhoogde connectiviteit zien tussen de dorsale anterieure cingulate cortex (dACC) en taak-specifieke corticale gebieden wanneer er een grote inspanning vereist is. Dit impliceert dat dACC, samen met de anterieure insula en intrapariëtale sulcus, een circuit vormt dat actief wordt wanneer de cognitieve inspanning groot is, en dat dACC verbinding maakt met gespecialiseerde hersengebieden, afhankelijk van de specifieke kenmerken van de taak. Samen tonen deze studies 1) een gedragsmatige en 2) een neurale signatuur van temporele variaties in de toewijzing van inspannende cognitieve controle, en 3) dat de neurale implementatie van cognitieve inspanning verzorgd wordt door dACC-geïnitieerde sensitisatie van taakafhankelijke gebieden.

Content

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General introduction

Cognitive effort

Today’s society is becoming increasingly complex, with an almost endless flow of information targeting our brain. For example, at the extremely busy Shibuya train station in Tokyo, it can be a true challenge to detect the signs that direct you to the right platform. The station is attended by millions of commuters each day, hurrying from train to train to make it at work on time. While these people rush past you, flashing and loud advertisements fight for your attention. Amidst all these distractions, you must process the right information regarding time of departure, platform number, direction of the train, and type of ticket required. Processing this bulk of information efficiently is demanding and requires the investment of cognitive effort through a range of information processing skills. For example, to reach the right platform, we must selectively direct our attention to relevant signs, memorize specific events or items (e.g., the time of departure), and ignore irrelevant information (e.g., advertisements or signs in Japanese). This inevitably requires investment of cognitive effort. In a multidimensional and volatile world, investment of effort is crucial to align our behavior with our goals. It takes cognitive effort to navigate through a complex environment, complete an exam, or bring a fiery discussion to a good end. In these situations, effort is reflected in the amplification of cognitive activity in order to meet high cognitive demands (Inzlicht, Shenhav, & Olivola, 2018).

Although cognitive effort is omnipresent in everyday life, it is not that easy to provide an exact definition. Yet, there are several aspects to cognitive effort that may shape our understanding of it. Cognitive effort revolves around information processing, is characterized by controlled (versus automatized) behavior, comes with a cost, and is central to several pathologies. On the basis of these four aspects, the specifics of cognitive effort investment will be outlined below.

First, it is useful to frame cognitive effort in terms of information processing. Effort is limited, perhaps because it draws from a limited pool of cognitive resources. From this perspective, cognitive effort mediates between how well an actor can potentially perform on a task and how well the actor actually performs on that task. Effort then refers to the set of intervening processes that determine what level of performance will be realized (Shenhav et al., 2017). From this operationalization it becomes clear that cognitive effort is closely related to difficulty, with difficult tasks requiring more effort to resolve them. However, whereas difficulty is a property of the task, cognitive effort is a property of the actor (Inzlicht et al., 2018). Thus, a task can be difficult without the actor investing much effort into it.

Second, it should be realized that the cognitive activity that underlies cognitive effort can take many forms (Shenhav et al., 2017). For example, engagement in mental reasoning (Kahneman, 2003) and working memory maintenance (Baddeley, 2003; Braver, 2012) require cognitive effort. This is also true for switching between tasks with different kinds of demands (Monsell, 2003), or overriding actions or habits in favor of more appropriate responses (Miller & Cohen, 2001). The crucial aspect of these functions is that they cannot be executed automatically but require controlled processing. The distinction between automatic and controlled processes has a rich tradition in cognitive psychology. For example, Posner and Snyder (1975) and Shiffrin and Schneider (1977) differentiated automatic activation processes resulting from past learning versus associations and processes that are under current (conscious) control. Automatic behavior was further characterized as fast and effortless, while controlled processing was described as slow, effortful, and dependent on a limited-capacity central resource (see also Botvinick & Cohen, 2014). The idea of a limited capacity for controlled processing was also foundational to the working memory model of Baddeley and Hitch (Baddeley, 2003; Baddeley & Hitch, 1974), which contains a central executive system responsible for the control and regulation of cognitive processes. This system makes sure the appropriate cognitive processes are active, and intervenes when they go astray, for example when automatic behavior is compromised by the presence of distractions.

Contrasting automatic to controlled processes also laid the foundation for later frameworks that popularized the use of the term “cognitive control” for effortful controlled processing (see below), and connected control to specific brain structures such as the prefrontal cortex (PFC; Miller & Cohen, 2001) and anterior cingulate cortex (ACC; Botvinick, Braver, Barch, Carter, & Cohen, 2001). Cognitive control itself is a multidimensional construct and although it is not exactly clear why it is perceived as effortful, the general consensus is that engagement of cognitive control is the key ingredient of effortful behavior (Kool & Botvinick, 2018). Effortful tasks are nonautomatic, requiring controlled responses, and involve capacity-limited processes - all features that characterize cognitive control (Westbrook & Braver, 2015).

The third aspect that helps to define cognitive effort is that it is typically considered to be costly. For example, investment of cognitive effort leads to cognitive fatigue, which is regarded as aversive (Boksem & Tops, 2008; Inzlicht & Marcora, 2016; Müller & Apps, 2019). Consequently, although the accomplishment of a goal may be perceived as rewarding, the effort that must be invested to reach that goal is preferably avoided. For example, in an experiment where a choice had to be made between actions associated with different levels of cognitive demand, it was shown that participants had a consistent bias in favor of the less demanding action (Kool, McGuire, Rosen, & Botvinick, 2010). This result attests to the negative utility of cognitive effort, which indicates that effort is costly.

In recent years, the idea that cognitive effort is costly has motivated a relatively new approach that analyzes effort from an economic point of view. Basically, this neuroeconomic approach states that the decision to invest cognitive effort is a cost-benefit trade-off. For example, according to the expected value of control (EVC) theory, applying effortful control is costly but also increases the likelihood of completing a task successfully and obtaining a reward (Shenhav, Botvinick, & Cohen, 2013). The optimal level of effort to invest maximizes the difference between the expected payoff of an action and the expected cost. The invested effort should be high enough to have a fair chance of obtaining reward but not too high because this would inflate the cost associated to it and overshadow the potential reward. The EVC thus constitutes the difference between the estimated gains and costs of a given effort investment. Based on the EVC, an actor decides how much effort it is worthwhile to engage in a task. For example, a cognitive dual-task with many task switches is generally perceived as effortful because it requires substantial cognitive control (Kool & Botvinick, 2014; Monsell, 2003). The decision to engage in the task will depend on the difference between expected gain (the size of the reward and the probability of obtaining it) and expected effort cost (based on the frequency of switches). The EVC integrates these two parameters. If an actor decides that the EVC is high enough, she/he will engage in the task.

Neuroeconomic approaches such as EVC theory have rapidly gained popularity in recent years because they offer a normative perspective on how decisions about the investment of effort may be made (Botvinick & Cohen, 2014). For example, they offer a framework for the finding that participants require more reward to engage in an effortful task. This principle is sometimes coined effort discounting (Botvinick, Huffstetler, & McGuire, 2009), which means that the subjective value of a reward is decreased by the cost of the effort needed to obtain the reward (Shenhav et al., 2013; Verguts, Vassena, & Silvetti, 2015). This is true for both cognitive (Botvinick et al., 2009; Burke, Brunger, Kahnt, Park, & Tobler, 2013; Cavanagh, Masters, Bath, & Frank, 2014; McGuire & Botvinick, 2010; Schouppe, Demanet, Boehler, Ridderinkhof, & Notebaert, 2014) and physical effort (Croxson, Walton, Reilly, Behrens, & Rushworth, 2009; Klein-Flugge, Kennerley, Friston, & Bestmann, 2016; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Prevost, Pessiglione, Metereau, Clery-Melin, & Dreher, 2010).

Finally, the concept of cognitive effort is not only of importance for information processing and decision making, it is also central in several pathological conditions. For example, patients with schizophrenia or depression are less motivated to expend effort to obtain a reward (Culbreth, Moran, & Barch, 2018; Hartlage, Alloy, Vázquez, & Dykman, 1993; Treadway, Bossaller, Shelton, & Zald, 2012). Also, symptoms and personality traits such as anhedonia (McCarthy, Treadway, & Blanchard, 2015; Treadway, Buckholtz, Schwartzman, Lambert, & Zald, 2009), apathy (Bonnelle, Manohar, Behrens, & Husain, 2016; Le Heron, Apps, & Husain, 2018), and anergia (Cohen et al., 1999; Holroyd & Yeung, 2012; Walton, Bannerman, & Rushworth, 2002) have a clear link to disrupted willingness to invest effort and may be connected to the behavioral profile of neurocognitive diseases. For example, Parkinson's disease has been associated to a reduced motivation to invest cognitive effort, which may be manifested as apathy due to reward insensitivity (Chong et al., 2015; Le Heron, Plant, et al., 2018; Muhammed et al., 2016). A recent study also showed that effort avoidance correlated positively with lack of perseverance and negatively with positive urgency, distress intolerance, obsessive-compulsive symptoms, disordered eating, and intrusive thoughts (Patzelt, Kool, Millner, & Gershman, 2019). In short, these studies show that deviant effort investment, either too little or too much, can be a symptom of various mental illnesses or dysfunctional personality traits.

In summary, it is clear that the construct of cognitive effort is important in daily life, has motivated cognitive theorizing, and plays a central role in several pathological conditions. Cognitive effort is required to improve or maintain performance, is applied through controlled processes, and is costly. The current dissertation revolves around how precisely cognitive effort is implemented, both behaviorally and neurally. It departs from the tight connection between cognitive effort and cognitive control and deals with the temporal variations and neural organization of effortful control.

Cognitive control

Over the years, cognitive control has become an umbrella term for "a set of functions that regulate more basic attention-, memory-, language-, and action-related faculties and coordinate their activity in the service of specific tasks" (Botvinick & Braver, 2015, p. 84). As put forward earlier, cognitive control is needed whenever behavior cannot rely on automatic processes (Posner & Snyder, 1975; Shiffrin & Schneider, 1977). This is for instance the case when contradictory information evokes response conflict. In cognitive research, this setting is typically created in tasks where irrelevant and relevant task dimensions provide conflicting information. A classic example is the Stroop task (Stroop, 1935), where automatic reading of a color name (irrelevant dimension) has to be suppressed in favor of detecting the ink color of the word (relevant dimension).

Apart from resolving cognitive conflict, there are many more instances of cognitive control that are often closely related or consist of overlapping processes. For example, response inhibition involves the suppression of a planned or ongoing cognitive or motor action (Aron, 2007; Logan, 1994), interference control is the ability to exert selective attention to resist distracting stimuli (Diamond, 2013), and task switching requires frequent switching among a small set of simple tasks (Monsell, 2003). Cognitive effort and cognitive control are heavily intertwined and sometimes used interchangeably. However, they are not synonymous. Cognitive effort is not a specific process such as attention, memory, or reasoning, that can be used to actually solve a task. Cognitive effort regulates the degree to which these controlled processes are engaged. Although it has been suggested that there exist effortful behavior that does not require controlled processing, it is unclear what processes would underly this behavior instead (Robertson, Hiebert, Seergobin, Owen, & MacDonald, 2015). In the current dissertation, cognitive control is treated as the force through which cognitive effort is exerted (Shenhav et al., 2017). Put differently, cognitive effort reflects the intensity with which cognitive control is exerted (i.e., it can be low or high), while cognitive control is the type of effort that is applied (i.e., it is a specific process, such as resolving response conflict).

The effortful nature of cognitive control is supported by various observations, many of them based on the avoidance of control. As touched upon before, an extensive line of research showed that people will forgo rewards to avoid the mobilization of cognitive control (e.g., Botvinick & Braver, 2015; Dixon & Christoff, 2012; Kool et al., 2010; Westbrook & Braver, 2015; Westbrook, Kester, & Braver, 2013). Also, since control is mainly needed when expectations are violated (i.e., when automatic processes are insufficient or need to be overruled in a given context), people will try to exploit the structure of their environment to form accurate predictions so they can avoid control (Waskom, Frank, & Wagner, 2017). Further, the effortful nature of control has also been assessed through pupil size, which can be utilized as a measure of cognitive effort. In conditions where much cognitive control was needed, higher cognitive effort was measured through larger pupil diameters (Diede & Bugg, 2017).

The temporal dynamics of cognitive control

From neuroeconomic theories we can infer that effortful control is costly and therefore affects cost-benefit considerations of whether or not to invest it. The cost of control may also influence the way cognitive control is implemented at different time scales, or *when* control is applied. Cognitive control is not a stable process but instead tends to vary over time (Botvinick & Braver, 2015; Braver, 2012; Jiang, Heller, & Egner, 2014; Ridderinkhof, 2002). One reason for these fluctuations is that different contexts may require different control modes, which each come with specific cognitive demands.

The claim that cognitive control can operate on different time scales has been motivated by several behavioral indices that roughly range from transient to sustained control (for a review see Braem et al., 2019). A typical cognitive control task such as the Stroop task contains trials with two response dimensions. On congruent trials, both dimensions elicit the same response (e.g., the word RED written in red). On incongruent trials, the two dimensions elicit conflicting responses (e.g., the word RED written in blue). On incongruent trials, the highly automatized response to read the word must be overcome in favor of detecting the ink color. This requires cognitive control and comes at the cost of slower response time and decreased accuracy. The difference in response time or accuracy rate between incongruent and congruent trials constitutes the congruency effect (CE). A small CE is typically taken to reflect strong implementation of cognitive control.

The congruency sequence effect (CSE) is a modulation of the CE (Gratton, Coles, & Donchin, 1992). The CSE entails a smaller CE after an incongruent trial than after a congruent trial. One dominant theory for the CSE is that people increase their control after an incongruent trial, which diminishes conflict on the subsequent incongruent trial. This leads to improved performance (i.e., speeded response time or increased accuracy). After a congruent trial, control is relaxed, which impairs performance on a subsequent incongruent trial, because the relaxed control settings increase vulnerability to conflict (Botvinick et al., 2001). Since the CSE varies on a trial-by-trial basis, it is typically taken as an example of a fast-changing or transient adjustment of control.

There are also types of control that operate on longer time scales. For example, the CE is also modulated by the general conflict context. When the proportion of incongruent trials in a task is small (i.e., mainly congruent, or MC, contexts), the CE is larger than when the proportion of incongruent trials is large (i.e., mainly incongruent, or MI, contexts; Braver, 2012; Bugg & Crump, 2012; Logan & Zbrodoff, 1979). This proportion congruency effect (PCE) is thought to reflect the operation of two different control modes that operate on short or long time scales (Botvinick et al., 2001; Braver, 2012; Jiang et al., 2014; Ridderinkhof, 2002). In MC contexts, control is only required occasionally and hence transiently activated whenever it is needed. Because task performance in this context mainly relies on fast automatic behavior, this strategy results in optimal performance (i.e., fast response times and high accuracy) on the frequent congruent trials. However, on incongruent trials, performance is impaired because cognitive control is only activated when conflict has been detected. This transient, late-correction mechanism increases response times and errors on these rare incongruent trials. Contrarily, when incongruent trials are frequent, as in MI contexts, a transient control mode would lead to frequent delays and errors. In that case, sustained control is more optimal. In this mode, conflict is anticipated and control is sustained across a longer time scale. The anticipatory nature of sustained control disallows conflict to impair responses on the frequent incongruent trials of the MI context, leading to improved performance on these trials.

Motivated by the CE, CSE, and PCE, several theoretical frameworks and models have attempted to explain the temporal variations in control. For instance, the dual mechanisms of control theory explains the PCE through the existence of two qualitatively different control mechanisms. A reactive mechanism accounts for transient changes of cognitive control after a control-requiring event (e.g., conflict) or a cue signaling such event has been encountered, while a proactive mechanism sustains cognitive control across a series of trials (Braver, 2012; De Pisapia & Braver, 2006)[1]. The proactive control mode biases attention, perception and action systems in a goal-driven manner. For example, in a Stroop task, the goal to “report the ink color” will be maintained for the duration of a block of MI trials. Contrarily, the goal will only be reactivated occasionally (i.e., on incongruent trials) in a block of MC trials. Proactive, or sustained, control thus requires active maintenance of task goals, which is demanding because it taxes the capacity-limited working memory. This is different in a reactive, or transient, mode, where the actor only has to apply effortful control incidentally to overrule low-effort automatic behavior. Transient control is computationally efficient because resources are freed up in the intervals where no control is needed. Its disadvantage is that when the triggers that induce reactivation are insufficiently salient or discriminative, reactivation may fail (Braver, 2012). Further, whereas sustained control is not easily interrupted, transient control is susceptible to internal or external distraction.

The effortful nature of sustained control is supported by the finding that concurrent working memory demands impair sustained but not transient control (Kalanthroff, Avnit, Henik, Davelaar, & Usher, 2015), and by the finding that individuals with low working memory capacity are less inclined to apply proactive control than persons with high working memory capacity (Redick, 2014). Furthermore, incentives enhance shifts from transient to sustained control, probably to compensate the greater cost of the latter (Chiew & Braver, 2011, 2013; Jimura, Locke, & Braver, 2010; Locke & Braver, 2008). This is in line with neuroeconomic approaches that suggest that more reward is needed to engage in effortful behavior. Thus, the cost-benefit tradeoffs that are important for effort-based decision-making also apply to the selection of control mode. An actor may weigh the estimated cost of sustained control (e.g., the cost of actively maintaining goal representations) against internal estimates of how valuable the consequences of such a control strategy are for task performance. If this assessment is negative, effort-sparing transient control may be a better alternative, even though it may compromise performance (and hence lower the estimated outcome).

Despite the prominent position of time scale variations in various frameworks of cognitive control, no behavioral quantification of this time scale is available. Such an empirical measure could be informative because, currently, transient (reactive) and sustained (proactive) control are often presented as two qualitatively distinct phenomena. It is questionable, however, if this reflects a cognitive reality. For example, in terms of parsimony, it would be more efficient if both modes of control were integrated into a single mechanism (Jiang et al., 2014). In fact, a continuous behavioral

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[1] Note that in this dissertation, transient and sustained control are sometimes used interchangeably with reactive and proactive control, respectively (cf. chapter 3). Unless specified otherwise, transient control is equated to reactive control, while sustained control is equated to proactive control.

scale may be better capable to capture (subtle) differences in control mode in a dynamic way. This time-scale measure would also closely correspond to the amount of effort that an actor invests in the task, with short time scales being less effortful than long time scales. Ideally, the measure should also be suitable to investigate other parameters that are expected to affect cognitive control strategies, such as volatility of a context (Jiang et al., 2014), working memory capacity (Gulbinaite & Johnson, 2013; Redick, 2014), and clinical conditions such as depression (Grahek, Shenhav, Musslick, Krebs, & Koster, 2019), schizophrenia (Barch & Ceaser, 2012), and substance use disorders (Garavan & Hester, 2007; Wilcox, Dekonenko, Mayer, Bogenschutz, & Turner, 2014). In chapter 2, a behavioral quantification of the time scale of cognitive control is introduced.

Neural mechanisms of transient and sustained control

Besides the lack of a sensitive method for identifying the time scale of cognitive control, it is also not clear how different control modes are implemented in the brain. Early models on cognitive control mainly focused on the Stroop task (Cohen, Dunbar, & McClelland, 1990) and assigned important roles to dorsal anterior cingulate cortex (dACC) and lateral prefrontal cortex (lPFC). (Botvinick et al., 2001). Briefly, the models consisted of simple neural networks with input units (for word and color), associative units, and output units (for verbal responses). In these networks, automaticity is represented by a strong connection between word-input units and verbal-response units, biasing the actor to read aloud the word (instead of reporting the color). To overcome the default response to read aloud the word, the connection between color-input unit and verbal-response unit must be strengthened. This first requires the detection of conflict elicited by incongruent word and color, by a monitoring unit. It was suggested that this task is among the functions of dACC. When conflict is detected by dACC, a control unit is activated that represents the current task (i.e., “report color”). This control unit was linked to lPFC. When the control unit is active, lPFC instigates top-down support for the pathway from color unit to verbal-response unit. This primes the system to respond to the color and overcomes the bias to read the word.

Not surprisingly, the first seminal fMRI studies on the neural underpinnings of cognitive control were also mainly focused on dACC and lPFC, where dACC was appointed the role of conflict or error detector and lPFC the role of control employer (Botvinick et al., 2001; Carter et al., 2000; Kerns, 2006; Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000). For example, the neural implementation of the CSE was shown to involve conflict-related dACC activity on the current trial that drives behavioral adaptation and increases lPFC activity on the subsequent trial (Kerns et al., 2004). The specific neural implementation of the PCE was first demonstrated when dACC responses to incongruent (vs. congruent) trials appeared to be stronger in MC than in MI contexts (Carter et al., 2000). The interpretation of this finding is that in MC contexts, transient control is applied, reflected in a short-lived but strong upregulation of conflict-induced signal in dACC on incongruent trials only. In the MI context, control is sustained across both incongruent and congruent trials. This protects the actor against the perturbing effects of conflict, which is reflected in a smaller difference in dACC activity between incongruent and congruent trials. This effect has later been replicated (De Pisapia & Braver, 2006; Grandjean et al., 2012; Jaspar et al., 2016; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016).

The involvement of similar brain regions in transient and sustained control is consistent with the dual mechanisms of control framework that proposes that transient control should be reflected in transient activation of dACC and lPFC, while sustained control should be mirrored in sustained activation of lPFC (Braver, 2012). The transient mechanism is thought to reflect a conflict-induced activation of dACC followed by a bottom-up reactivation of task goals in lPFC. The sustained mechanism is believed to reflect the active maintenance of task goals by lPFC across a more extended period of time. Some fMRI studies have targeted this principle directly by statistically separating transient and sustained brain activation, and showed that indeed the same fronto-parietal regions were active on a transient or sustained scale, depending on whether the context was MC or MI (Braver, Reynolds, & Donaldson, 2003; Marini et al., 2016; Wilk, Ezekiel, & Morton, 2012). These regions included medial frontal cortex (MFC, including dACC) and lPFC, but also precuneus and parietal areas. Other studies have also claimed that control modes with different temporal profiles exist but that these are implemented by different brain areas (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Olsen et al., 2010; Seeley et al., 2007; Wilk et al., 2012). For example, it has been argued that dACC and anterior insula (AI) have an important role in the stable maintenance of task-sets, as opposed to the rapid control adjustments implemented by other fronto-parietal areas (Dosenbach et al., 2007, 2006; Gratton, Sun, & Petersen, 2018; see also Holroyd & Yeung, 2012).

Independent of the question whether transient and sustained control are applied by the same or different brain structures, dual-mode frameworks of control agree on the existence of temporal variations in cognitive control. Crucially, an important prediction that can be derived from these frameworks is that if control indeed can be applied in a sustained way, it should be detectable in the intervals between trials. After all, a truly sustained control mode is of an anticipatory nature, which means it should be mirrored in increased brain activation, not only during trial performance but also before a trial is encountered. It is exactly this property that makes sustained control more effortful than transient control, and the reason why it is avoided if possible.

Previous work that measured brain activity in the intertrial interval (ITI) was mainly targeted at fast-changing sequential effects. For example, Horga and colleagues (2011) showed that activity in the medial- and dorsolateral PFC during the ITI scaled with the number of previously encountered conflict trials. This neural system also affected subsequent conflict processing on a trial-by-trial basis. There have also been a few electroencephalography (EEG) studies that showed decreased alpha (Compton, Arnstein, Freedman, Dainer-Best, & Liss, 2011) or increased theta power (Pastötter, Dreisbach, & Bäuml, 2013; van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015) in the ITI following an incongruent trial (vs. after a congruent trial). Because alpha oscillations have been interpreted as an inverse index of cerebral activity and theta oscillations as an index of controlled processes (Cavanagh & Frank, 2014), both results imply greater cerebral activity when control is intensified after an incongruent trial, in anticipation of the next trial. Closely related to this upregulation of control during the ITI is cue-induced preparation. fMRI studies have shown anticipatory activation of parietal cortex, lPFC, and dACC in response to cues signaling the need for control (Aarts, Roelofs, & van Turennout, 2008; Stern, Wager, Egner, Hirsch, & Mangels, 2007). Together, these studies show that neural mechanisms of anticipatory control can be detected in the ITI.

Whether anticipatory control can also be detected between trials in contexts that demand high (i.e., MI) or low effort (i.e. MC) is yet unclear. This translates to the question whether transient and sustained control modes indeed have their own neural signature and generalizes to the question whether the temporal dynamics of control depend on the effort demand of the context. If so, neural activity in the ITI should be stronger in MI than in MC contexts. The follow-up question then is if both control modes indeed involve similar brain regions activated at different time scales. These questions will be addressed in chapter 3.

The neural implementation of cognitive effort investment

Whereas the temporal dynamics of cognitive effort through allocation of cognitive control are concerned with the question *when* cognitive effort is invested (or: how much at what moment), another important question is *how* effort investment is implemented (or: through what neural mechanism). It seems a crucial role in this matter is played by dACC. Over the past two decades, the role that literature ascribed to dACC has evolved from a detector of conflict or error (Botvinick et al., 2001; Bush, Luu, & Posner, 2000) to an area that is engaged in effortful behavior more generally (Botvinick, Cohen, & Carter, 2004; Holroyd & Yeung, 2012; Shenhav et al., 2013). This evolution was partly motivated by the fact that although some studies have shown a disturbed CE or CSE after dACC lesions in humans (e.g., Swick & Jovanovic, 2002), many have not (e.g., Baird et al., 2006; Fellows & Farah, 2005; Stuss, Floden, Alexander, Levine, & Katz, 2001). A more consistent finding is the general slowing of responding by dACC-lesioned patients, across tasks and independent of conflict (Alexander, Stuss, Shallice, Picton, & Gillingham, 2005; Fellows & Farah, 2005; Picton et al., 2007; Stuss et al., 2005;

Yeung, 2013). In fact, there is a body of evidence that associates dACC lesions to a lack of motivation or anergia (e.g., Cohen et al., 1999; Holroyd & Yeung, 2012; Walton, Bannerman, & Rushworth, 2002). This has led to the critique that relating dACC to response conflict (and error monitoring) is too restrictive and that dACC in fact provides a more general signal that is necessary to energize many cognitive control actions (Holroyd & Yeung, 2012). If we take conflict and errors to be signs of increased cognitive demand, then dACC activity in response to these events may in fact be a response to proxies for increased effort requirement (Shenhav et al., 2017).

The role of dACC in effort investment is supported by a wealth of research. Model simulations have shown that dACC-lesioned rats are less likely to engage in effortful behavior (Holroyd & Mcclure, 2015). dACC activity has also been related to anticipation of effortful tasks (Chong et al., 2017; Croxson et al., 2009; Kurniawan et al., 2013; Prevost et al., 2010), self-reported effort investment (Mulert, Menzinger, Leicht, Pogarell, & Hegerl, 2005), and will to persevere (Parvizi, Rangarajan, Shirer, Desai, & Greicius, 2013). Several studies also corroborate the idea that effort-based cost-benefit values are computed by dACC (Botvinick et al., 2009; Chong et al., 2017; Croxson et al., 2009; Massar, Libedinsky, Weiyan, Huettel, & Chee, 2015; Westbrook, Lamichhane, & Braver, 2019).

Based on these and other findings, recent frameworks have suggested a hierarchical organization of effort allocation, with dACC at a high position in this hierarchy. Generally, the models apply neuroeconomic principles in the sense that they maximize the (subjective) value of an action by weighing expected outcomes against expected costs. For example, the model by Holroyd and Yeung (2012) suggests that dACC is involved in the control of actions over extended periods. dACC is thought to mitigate the short-term cost of effortful actions in favor of longer-term rewards that will be obtained after completing a current sequence of actions. Hence, the model maximizes long-term value by selecting actions while dACC-initiated control protects those actions from being delayed or overturned by the effort they require. In this model, dACC can be seen as the provider of an energizing signal necessary to perform a sequence of effortful actions. In the model by Verguts and colleagues (2015), dACC integrates the internal estimates of values and effort costs to determine whether or not to allocate effort to an action. The EVC model by Shenhav and colleagues (2013) also contrasts the expected reward against the expected cost to compute the value of an action. Although strictly not hierarchically organized, the EVC model claims that activity in dACC tracks the amount of control that is determined to be worth to invest, given an expected payoff. Hence, dACC is thought to optimize effort allocation by selecting the action that maximizes the subjective value of an action. It determines which task is best to perform (i.e., the identity of the control signal) as well as the amount of effort to allocate (i.e., the intensity of the control signal).

Models on effort investment have in common that effort (cost) is processed separately from the task to be solved (Holroyd & Yeung, 2012; Shenhav et al., 2013; Verguts et al., 2015). Generally, dACC is thought to specify which task to perform and what level of effort or type of control to apply. Solving the specific task, however, is subserved by other specialized brain areas. This implies that dACC should scale with effort demand, independent of the specifics of the cognitive task. Indeed, dACC is shown to be active on a wide range of tasks that demand some type of cognitive control (Corbetta & Shulman, 2002; Dosenbach et al., 2006; Engström, Karlsson, Landtblom, & Craig, 2015; Menon & Uddin, 2010; Nelson et al., 2010; Shenhav et al., 2017). Crucially, this activity occurred in paradigms where cost-benefit decision-making is not a factor. This suggests that in addition to the processing of effort costs in order to optimize effort-based decision making (Engström et al., 2015; Shenhav et al., 2013; Vassena et al., 2014; Westbrook et al., 2019), dACC's task is also to energize task engagement (Holroyd & Yeung, 2012; Kouneiher, Charron, & Koechlin, 2009).

In sum, it is plausible that dACC plays a crucial role in effort investment in two ways. First, as part of a broader network of brain regions, dACC may track the expected effort demand of a task. When this demand is high, dACC becomes more active, independent of the type of cognitive task. Second, dACC may exert its effect on task processing by energizing specialized upstream areas required to solve the task at hand. If this is correct, then dACC activity should be associated with the engagement of task-specific neural systems. This association should be stronger when the effort required to perform a task is high. These principles are assessed in chapter 4.

Research objectives and outline of the dissertation

As has become clear in this general introduction, cognitive effort is crucial for many aspects in daily life and takes a prominent role in information processing. Cognitive effort is almost inseparable from cognitive control, which can be considered the function through which cognitive effort is exerted. Cognitive control can be applied on different temporal scales, which may have their own neural signature. The investment of effortful control involves dACC, which may track effort costs and fuel upstream brain areas that implement task-specific processes, when effort requirement is high. In this dissertation, three main questions revolving around the temporal dynamics of cognitive control and the neural implementation of cognitive effort will be answered in three separate chapters.

In **chapter 2**, the focus is on time scale variations in cognitive control. A method inspired by reinforcement learning is introduced to investigate how control modes operate on different time scales. Briefly, in this study, the CSE was extended from one trial to multiple trials into the past to quantify the influence of previous trials on current-trial performance as a function of trial distance. The rate at which this influence changed across trials was taken as a measure of the time scale of control. The method was applied to a flanker task with different conflict frequencies and volatility. In agreement with theories differentiating transient from sustained control, the results show that the time scale of control was shorter in rare-conflict and volatile contexts.

The fMRI study in **chapter 3** builds on these findings and aims to clarify the neural underpinnings of time scale differences in control. A cognitive control task with MC and MI contexts was administered to healthy participants. On-trial and between-trial activity were compared between contexts to differentiate transient and sustained control. Increased on-trial fronto-parietal activity was found on incongruent trials in the MC versus the MI block, indicating increased transient activity when cognitive control was required rarely. Increased between-trial activity was found to be larger in similar regions in the MI block versus the MC block. This implies increased sustained activity when cognitive control was required frequently. These results illuminate how context-dependent transient and sustained control subtend the same brain areas but operate on different time scales.

Whereas chapters 2 and 3 deal with the temporal dynamics of cognitive effort through allocation of cognitive control (i.e., *when* cognitive effort is applied), **chapter 4** focuses on *how* effort investment is implemented neurally. In the fMRI study in this chapter, healthy participants performed two perceptual decision tasks that required them to detect either faces or houses, under low or high effort demand. Results showed a network of dACC, AI, and intraparietal sulcus (IPS) to be more active when effort demand was high, independent of the performed task. Importantly, effort demand modulated functional connectivity between dACC and face- or house-responsive perceptual areas, depending on the task at hand. This highlights the crucial role of dACC in generic effort investment and suggests that the neural implementation of cognitive effort involves dACC-initiated sensitization of task-dependent areas.

Finally, in **chapter 5** these findings are connected, critically evaluated, and framed in existing literature. The broader significance of the findings is highlighted and avenues for future research are suggested.

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2

Beyond trial-by-trial adaptation: A quantification of the time scale of cognitive control

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Abstract

The idea that adaptation to stimulus or response conflict can operate over different time scales takes a prominent position in various theories and models of cognitive control. The mechanisms underlying temporal variations in control are nevertheless poorly understood, which is partly due to a lack of appropriate empirical measures. Inspired by reinforcement learning models, we developed a method to quantify the time scale of control behaviorally, by computing trial-by-trial effects that go beyond the preceding trial. Briefly, we extended the congruency sequence effect from one trial to multiple trials into the past and quantified the influence of previous trials on current trial performance as a function of trial distance. The rate at which this influence changes across trials was taken as a measure of the time scale of control. We applied the method to a flanker task with different conflict frequencies and volatility. Results showed that the time scale of control was smaller in rare-conflict and volatile contexts, compared to frequent-conflict and neutral contexts. This is in agreement with theories differentiating transient from sustained control modes. The method offers new opportunities to reveal temporal differences in control modes and can easily be applied to various empirical paradigms.

Keywords

Cognitive control; Conflict; Congruency sequence effect; Trial-by-trial adaptation; Conflict adaptation

Introduction

The ability to flexibly adjust behavior to the demands of the environment is crucial for efficient goal achievement. For example, when faced with conflicting response options, we need cognitive control to overcome automatic response tendencies in favor of more appropriate behavior. Several theories have suggested that cognitive control can operate on different time scales (e.g., Braver, 2012; Jiang, Heller, & Egner, 2014; Ridderinkhof, 2002). These scales can range from a fast-changing adjustment of control on a trial-by-trial basis (e.g., Gratton, Coles, & Donchin, 1992) to a more stable control mode that is sustained over multiple trials (e.g., Bugg & Chanani, 2011; Jimura, Locke, & Braver, 2010). Temporal variations are often used to explain differences in cognitive control between individuals and conditions (e.g., Appelbaum, Boehler, Davis, Won, & Woldorff, 2013; Funes, Lupiáñez, & Humphreys, 2010; Purmann, Badde, & Wendt, 2009). However, the lack of a behavioral quantification of these time scales has hampered progress.

Several measures of cognitive control have been introduced over the past decades. The congruency effect (CE), for example, reflects slower response times (RTs) and lower accuracy on conflict trials (i.e., incongruent trials), compared to trials without conflict (i.e., congruent trials). A classic example of the CE is the Stroop effect, where ink color and word name can be congruent (e.g., the word RED printed in red) or incongruent (e.g., the word RED printed in green; Stroop, 1935).

Modulations of the CE are often used to infer the time scale of control. For example, the CE is subject to trial-by-trial adaptations, meaning that conflict not only affects performance on the current trial but also on the next one. This is reflected in the congruency sequence effect (CSE), which entails a smaller CE when the preceding trial is incongruent, compared to congruent (Gratton et al., 1992; for reviews see Duthoo, Abrahamse, Braem, Boehler, & Notebaert, 2014; Egner, 2007). The CSE has been ascribed to conflict-driven adaptation of control (Botvinick, Braver, Barch, Carter, & Cohen, 2001). After an incongruent trial, control is increased, which diminishes interference on the subsequent incongruent trial. A congruent trial results in a decrease of control and hence increases the vulnerability to conflict on the next trial. The conflict adaptation effect measured by the CSE thus reflects the continuation of control over two trials and in that sense indexes anticipatory and sustained control. Nevertheless, the range of this effect is small, capturing only trial-by-trial adjustments and not variations in control over a longer time scale.

The interpretation of the CSE in terms of cognitive control is not without controversy. Alternatively, it has been claimed that the CSE is due to associative mechanisms driven by the repetition or integration of stimulus or response features (i.e., repetition account; Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003). Current consensus however seems to be that the CSE embodies both stimulus-specific repetitions and cognitive control mechanisms (for reviews see Duthoo et al., 2014; Egner, 2007) and it has been proposed that cognitive control is in fact built on repetitions of stimulus, response, and control features (Verguts & Notebaert, 2009).

The CE is not only modulated by conflict on the previous trial but also by the general conflict context, or the proportion of (in)congruent trials within a block (Bugg & Crump, 2012; Logan & Zbrodoff, 1979). The proportion congruency effect (PCE) entails that the CE is larger in blocks with mainly congruent (MC) trials than in blocks with mainly incongruent (MI) trials. This has been interpreted as a behavioral marker for transient control in MC blocks, involving short upregulations of control in response to rare incongruent trials, and sustained control in MI blocks, involving stable control that is less subject to trial-by-trial adaptations (e.g., De Pisapia & Braver, 2006; Kane & Engle, 2003). Although this explanation for the PCE has been challenged by accounts referring to item-specific control (Jacoby, Lindsay, & Hessels, 2003) and contingency learning (Schmidt & Besner, 2008), recent findings do emphasize a role for block-wide strategic control in the PCE (e.g., Bugg et al., 2015; Bugg, McDaniel, Scullin, & Braver, 2011; Entel, Tzelgov, & Bereby-Meyer, 2014; Torres-Quesada, Funes, & Lupiáñez, 2013). The exact mechanism behind this effect is nevertheless still unclear. For example, it is not known how many trials in the past drive the PCE or how the influence of previous trials on the current trial is affected by the temporal distance between them. Besides, while the CSE is bound to the previous trial by definition, the behavioral extent of the PCE is not clearly delineated. Hence, with the CSE and PCE, we have two measures at our disposal that each lack sensitivity to identify variations in the time scale of control.

The evaluation of temporally different control modes is hampered by this empirical ambiguity. This is problematic because variations in time scales are assumed in several models of cognitive control. The Dual Mechanisms of Control (DMC) model, for example, explains the PCE by two control mechanisms that operate on different time scales (i.e., reactive and proactive control; Braver, 2012; De Pisapia & Braver, 2006). Other models suggest that performance on the current trial is the result of the accumulation of effects of previous (in)congruent trials (Botvinick et al., 2001; Verguts & Notebaert, 2008). Specifically, control is adjusted based on a weighted average of conflict on all preceding trials, explaining both the CSE and PCE in a single cognitive control system. A time scale parameter determines the relative importance of recent versus more remote trials (Botvinick et al., 2001). The model by Jiang and colleagues (2014) in addition allows this time scale parameter to adapt as a function of trial history.

Summing up, although time scale variations are crucial in models and theories of cognitive control, no behavioral measurement of this time scale exists. To fill this gap, we introduce a method based on a statistical model for the effect of the previous trial on the current trial (i.e., CSE) and extend this to the effect of more remote trials. Briefly, the trial-by-trial adaptation captured by the CSE is reflected in the interaction between current and previous congruency, $C_i \times C_{i-1}$, where variable C_i indicates congruency status (0 = congruent, 1 = incongruent) on trial i (Notebaert & Verguts, 2007). In our method, regressors are added to this statistical model to capture the interaction between current congruency and congruency on more remote trials ($C_i \times C_{i-2}$, $C_i \times C_{i-3}$, etc.). We then assess how strongly the effects of previous trials decrease as a function of trial distance (see Figure 1). In this way, the degree to which previous trials affect the current trial as a function of trial distance can be computed.

Inspiration for this method was found in the reinforcement learning literature (e.g., Behrens, Woolrich, Walton, & Rushworth, 2007; Bromberg-Martin, Matsumoto, Nakahara, & Hikosaka, 2010; Silvetti, Seurinck, van Bochove, & Verguts, 2013). Here, models predict reward learning rates based on the outcome of previous trials. The learning rate can be conceptualized as a “window size”, or the number of previous trials that is taken into account. The smaller the window size, the fewer trials in the past are used to predict current reward. In a similar vein, window size can be used as a measure for the time scale of control. In this case, a small window (steep curve in Figure 1, dashed line) entails that performance on the current trial is mostly affected by experienced conflict on the preceding trial and less by more remote trials. This is indicative of a transient control mode operating on a short time scale. A large window (flatter curve in Figure 1, solid line) entails that performance on the current trial is also affected by conflict on more remote trials. This is indicative of a more sustained control mode operating over a longer time scale.

We applied our method using a flanker task with four different blocks with varying proportions of congruent and incongruent items: 1) a neutral block with 50% congruent items; 2) an MC block with 80% congruent items; 3) an MI block with 20% congruent items; 4) a volatile block, where the proportion congruency changed every 20 trials. We hypothesized that in MC blocks, control would operate on a short time scale, reflected in fast adjustments in control and hence a small window. In MI blocks, slower updating and thus a larger window was expected, indicating control operating over a longer time scale (De Pisapia & Braver, 2006). A volatile block was added since it has been suggested that volatility increases learning rates (Behrens et al., 2007; Jiang et al., 2014) and hence may also elicit shorter time scales of control.

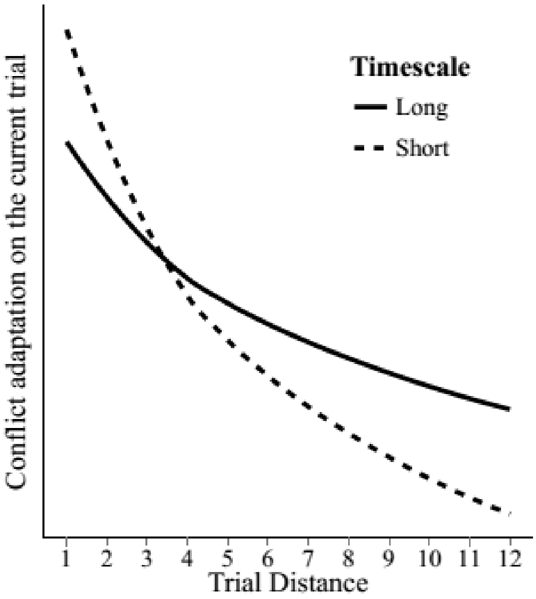

Figure 1. Hypothetical influence of previous conflict on the current trial. The plot shows conflict adaptation (i.e., the interaction between current and previous congruency) as a function of trial distance. For example, when trial distance is 5, the corresponding value on the y-axis represents the interaction between congruency on the current trial and congruency on the fifth trial back (i.e., $C_i \times C_{i-5}$). The dashed curve represents a situation where the current trial is mainly affected by the most recent trials (i.e., trials with a small distance to the current trial). The steep slope of this curve indicates that effects of previous trials quickly decline with increasing trial distance, which reflects a small window of control. This implies that control is applied over a short time scale. The solid curve represents a situation where, compared to the dashed curve, performance on the current trial is less affected by recent trials and more by remote trials. The gradual decline of this curve indicates a large window, or the exertion of control over a longer time scale.

Method

Participants

Forty-five participants were recruited from the participant pool at the Vrije Universiteit Brussel. All participants gave written informed consent and received a course credit or monetary reward for participation. Participants with overall error rates larger than 25% were excluded (*n* = 3), leaving 42 subjects included for analysis (32 female, mean age = 22.29 ± 5.77).

Material and procedure

An arrow flanker task was used consisting of a central target arrow flanked by two distractor arrows on both sides. Congruent (i.e., <<<<< and >>>>>) and incongruent (e.g., <<><< and >><>>) flanker stimuli (4° wide and 1° high) were presented in white against a black background in the center of the screen. Participants were instructed to press a left or right button on a response box (Cedrus RB-840) with their corresponding index finger as fast and as accurately as possible in response to the central target arrow. Each trial started with a 500ms fixation cross, followed by 500ms blank screen. This was followed by the flanker stimulus, which remained on the screen until the participant responded. No feedback was given.

Four different blocks of 160 trials each were created with different proportions of congruent and incongruent trials. In the neutral, MC, and MI block, the ratio congruent:incongruent trials was 50:50, 80:20, and 20:80, respectively. In the volatile block, the overall ratio was 50:50, but the ratio changed every 20 trials between 80:20 and 20:80. Presentation of the trials in each block was random. Each subject completed all block types; block order was counterbalanced across subjects using a Latin square. Blocks were separated by a 60 second pause.

Before the experiment, we explained to participants that there were easy (i.e., congruent) and difficult (i.e., incongruent) trials, and blocks with mainly easy, mainly difficult, or an equal number of easy and difficult trials. Participants were asked after each block whether they thought the previous block contained mainly easy trials, an equal number of easy and difficult trials, or mainly difficult trials. Answers were given on a scale from 1 to 3 (1 = mainly easy, 3 = mainly difficult).

Prior to the main experiment, participants completed 16 practice trials (50% congruent) with accuracy feedback, followed by a practice question about the ratio of easy and difficult trials.

Analysis

The following trials were excluded: the first trial of each block (0.63%), error trials (2.79%), trials following errors (2.59%), and trials faster than 250ms (0.03%) or slower than 1500ms (0.32%).

Next, RTs (in ms) were inverse transformed (1/RT) to better approximate the normal distribution. Inverse transformed RTs were multiplied by -10000 to restrict the number of decimal places. This way, larger inverse RTs reflect slower responses and uninformative decimals are lost, thus facilitating interpretation (Kinoshita, Mozer, & Forster, 2011).

First, conventional analyses of the PCE and CSE were performed. The mean RTs were entered in a repeated measures ANOVA with the factors block type (neutral, MC, MI, or volatile), current-trial congruency (congruent or incongruent), and previous-trial congruency (congruent or incongruent) as within-subjects factors. Greenhouse-Geisser correction was applied when the assumption of sphericity was violated.

Second, for the time scale analyses, the RTs were analyzed on trial level in two steps. In a first step, multiple regression was performed with RT as dependent variable. The predictors included in the model were congruency of the current trial (C_i), congruency of the 12 preceding trials (C_{i-k} where k = 1, ..., 12 represents the trial distance from the current trial i), and the interactions between current-trial congruency and preceding-trial congruency ($C_i C_{i-k}$), resulting in the statistical model:

$$RT = \beta_0 + \beta_1 C_i + \beta_2 C_{i-1} + \beta_3 C_{i-2} + \ldots + \beta_{13} C_{i-12} + \beta_{14} C_i C_{i-1} + \beta_{15} C_i C_{i-2} + \ldots + \beta_{25} C_i C_{i-12}$$

Each variable C_i could take on the value of 0 (for congruent) or 1 (for incongruent). Of key interest were the effects of previous trials on the current trial, reflected in the interaction terms $C_i C_{i-k}$. These interaction terms capture the degree to which congruency on trial $i-k$ affects adaptation on the current trial (i). It can be considered an extension of the CSE from one trial into the past to 12 trials into the past (while controlling for the other variables in the model). The regression analysis was performed separately for each block of trials within every participant (R code available in Supplemental Material).

In the second step, the 12 regression coefficients of the interaction terms ($C_i C_{i-k}, k = 1 \ldots 12$) estimated by the model of step 1 for each block type and participant were entered as dependent variables in a linear mixed model with the continuous variable trial distance (1-12) and the factor block type (neutral, MC, MI, or volatile) as fixed predictors. We will refer to the dependent variable as the conflict adaptation weight. The predictor trial distance was log transformed (log trial distance) to improve fit to the non-linear relation between trial distance and conflict adaptation weight. It was subsequently mean-centered to allow interpretation of the intercept (i.e., the intercept then reflects the conflict adaptation weight of the average log trial distance). The neutral block was taken as the reference level for the block type predictor. The model was extended stepwise and each model was compared to its initial model to test for significance of the added predictor. Akaike information criterion (AIC; Akaike, 1974) is reported as a measure of model fit with lower values indicating a better fit. This measure penalizes model complexity which implies that more complex models are only favored if they explain the data substantially better than the simpler model. Models were statistically compared using the likelihood ratio (χ^2). All models included a random intercept for participant and were fitted using maximum likelihood in the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015) for R (R Core Team, 2015).

Results

Conventional analysis of PCE and CSE

Repeated measures ANOVA with the within-subject factors block type (neutral, MC, MI, or volatile), congruency (congruent or incongruent), and previous congruency (congruent or incongruent) revealed main effects of block type, *F*(2.39, 97.98) = 3.78, *p* = 0.020, congruency, *F*(1, 41) = 657.04, *p* < 0.001, and previous congruency, *F*(1, 41) = 9.07, *p* = 0.004. The main effect of congruency indicates a CE.

Block type and congruency interacted significantly, *F*(2.30, 94.41) = 43.57, *p* < 0.001, indicating a PCE. To study this effect in more detail, CEs were computed and compared between blocks using paired sample *t*-tests (see Figure 2a). This revealed that the CE was smallest in the MI block and increased gradually over the neutral block, the volatile block and the MC block. More specifically, a smaller CE was observed in the MI block compared to all other blocks (respectively, neutral block, *t*(41) = 5.22, *p* <.001; volatile block, *t*(41) = 8.25, *p* <.001; MC block, *t*(41) = 12.64, *p* <.001). A smaller CE was also found in the neutral block compared to the volatile block, *t*(41) = 4.19, *p* <.001, and MC block, *t*(41) = 13.23, *p* <.001. The CE was also smaller in the volatile block compared to the MC block, *t*(41) = 10.52, *p* <.001.

No two-way interaction was found between block type and previous congruency, *F*(2.49, 102.06) = 0.93, *p* = 0.43, but congruency and previous congruency did interact, *F*(1, 41) = 138.10, *p* < 0.001, pointing at a smaller CE after an incongruent trial than after a congruent trial, or a CSE. This CSE was modulated by block type, as evident in the three-way interaction between block type, congruency, and previous congruency, *F*(2.56, 105.12) = 6.96, *p* < 0.001. To specify this three-way interaction, CSEs were computed and compared between blocks using paired sample *t*-tests (see Figure 2a). A smaller CSE was found in the MI block compared to the volatile block, *t*(41) = 2.81, *p* = 0.007, and the MC block, *t*(41) = 3.23, *p* = 0.002. The CSE was also smaller in the neutral block compared to the volatile block, *t*(41) = 4.12 *p* < 0.001, and the MC block, *t*(41) = 3.74, *p* < 0.001. The other comparisons revealed no significant effects (both *p*'s > .74). One-sample *t*-tests indicated that, despite these differences between blocks, the CSE remained significant in all blocks (all *p*'s < .001).

The time scale of control

Table 1 displays the fitted statistical models and comparisons of each model relative to the prior one. Results show that the model with a main effect of log trial distance (model 1) explained the data better than the null model with only an intercept, $\chi^2(1) = 119.9$, *p* < 0.001. A model with a main effect of block type (model 2) also explained the data better than the null model, $\chi^2(3) = 30.5$ *p* < 0.001.

Entering both main effects in one model (model 3) resulted in a better model fit than a model with only log trial distance, model 1, $\chi^2(3) = 32.6$, $p < 0.001$, or only block type, model 2, $\chi^2(1) = 121.9$, $p < 0.001$. Allowing the main effects to interact (model 4) further improved model fit compared to model 3, $\chi^2(3) = 8.5$, $p = 0.037$. The regression coefficients of the optimal model 4 are displayed in Table 2. Figure 2b displays the estimates of model 4, corrected for the intercept of each condition.

Planned linear contrasts (one-sided) were computed for pairwise comparisons of the slopes (i.e., time scales) of the four conditions, estimated by model 4. Since the neutral block was set as the reference level, the slope of this condition is reflected in the estimate for log trial distance. The slopes of the other three conditions are the sums of the estimate for log trial distance and each interaction term (Table 2). For example, the slope of the MC block equals the slope for log trial distance, adjusted by the estimate for log trial distance × Block MC. Pairwise comparisons revealed a smaller slope for the MI block (0.51) compared to the volatile block (0.89), $z = 2.02$, $p = 0.022$, and the MC block (0.98), $z = 2.49$, $p = 0.006$, but not compared to the neutral block (0.61), $z = 0.50$, $p = 0.33$. The slope in the neutral block was also smaller than the slope of the MC block, $z = 1.99$, $p = 0.023$. A trend towards a smaller slope for the neutral block compared to the volatile block was found, $z = 1.51$, $p = 0.065$. The volatile and MC block did not differ in slope, $z = 0.48$, $p = 0.32$. These differences in slopes are reflected in Figure 2b. To check if the conflict adaptation weight varied with trial distance for every block type, a model with log trial distance was compared to a model without log trial distance (i.e., the null model) for each block type separately. This revealed that trial distance indeed predicted the conflict adaptation weight in each block (all *p*'s < 0.01).

Linear contrasts were also computed for pairwise comparisons of the main effect of each block type (i.e., the conflict adaptation weight of the average log trial distance), estimated by model 4 (Figure 2c). Here, the main effects for the MC, MI, and volatile block are computed by adjusting the main effect of the neutral block (i.e., the intercept) by the main effect of the MC, MI, or volatile block (Table 2). Compared to the MC block (-1.09), the main effects were smaller (i.e., less negative) in the volatile block (-0.52), $z = 4.20$, $p < 0.001$, the neutral block (-0.38), $z = 5.19$, $p < 0.001$, and the MI block (-0.49), $z = 4.45$, $p < 0.001$. No other contrasts for the main effect of block were significant (all *p*'s > .32).

Proportion congruency awareness

Finally, we checked whether subjects were aware of the differences in proportion congruency between blocks[2]. Friedman's ANOVA revealed that this was indeed the case, $\chi^2(3) = 66.74$, $p < 0.001$. Post-hoc Wilcoxon Signed Rank tests showed that the median rating for the MI block (median rating =

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[2] These analyses were performed on 34 subjects because the rating scores of eight subjects were missing due to a technical failure.

3) was higher than the median ratings for the neutral block (median rating = 2), $Z = 3.56$, $p < 0.001$, the volatile block (median rating = 2), $Z = 4.26$, $p < 0.001$, and the MC block (median rating = 1), $Z = 5.07$, $p < 0.001$. Furthermore, the median rating for the neutral and volatile blocks were higher compared to the MC block, $Z = 5.06$, $p < 0.001$, and $Z = 4.56$, $p < 0.001$, respectively. No difference in rating was found between the neutral and volatile block, $Z = 0.23$, $p = 0.82$.

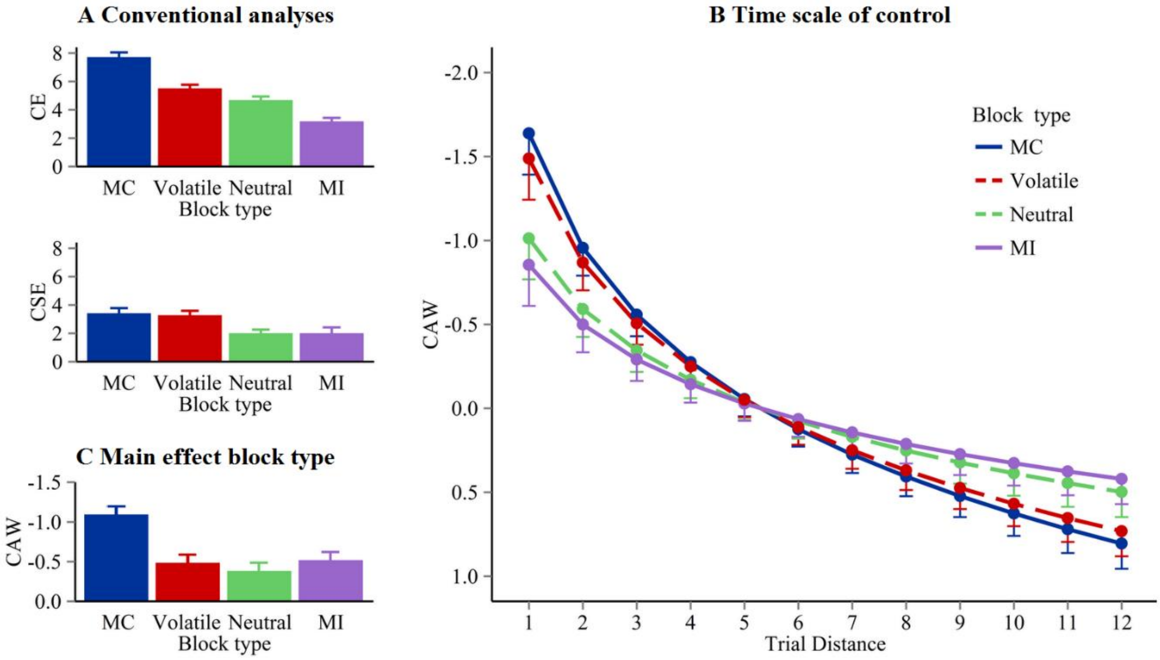

Figure 2. Results of time scale and conventional analyses. *A.* Congruency effects (CEs) and congruency sequence effects (CSEs) per block type, expressed in mean inverse transformed RTs (i.e., -10000/RT). *B.* Model estimates (each pair of points connected by piecewise linearly interpolated lines) of model 4. Each condition is plotted after subtracting its intercept. The original scale of trial distance is displayed on the x-axis, not log trial distance (which was included in the linear mixed models for statistical testing). This way, the non-linear relationship between trial distance and conflict adaptation weight is maintained in the figure. *C.* Main effect of block type (i.e., the conflict adaptation weight of the average log trial distance). Error bars represent standard errors of the mean. CAW = Conflict Adaptation Weight; MC = mainly congruent; MI = mainly incongruent.

Table 1. *Model comparisons.*

	Model	*df*	AIC	log lik.	Test	χ^2	*p*
0.	(intercept)	3	9016	-4505			
1.	log trial distance	4	8998	-4445	1 vs. 0	119.85	< .001
2.	block type	6	8991	-4490	2 vs. 0	30.55	< .001
3.	log trial distance + block type	7	8871	-4429	3 vs. 1	32.64	< .001
					3 vs. 2	121.94	< .001
4.	log trial distance + block type + log trial distance × block type	10	8869	-4424	4 vs. 3	8.48	.037

Note. AIC = Akaike information criterion; log lik. = log Likelihood.

Table 2. *Coefficient estimates of linear mixed model 4 with conflict adaptation weight predicted by log trial distance, block type (neutral, MC, MI, volatile) and their interaction. Neutral block type served as reference level.*

Variable	Estimate (SE)	*t*
(intercept)	-0.38 (0.10)	-3.74
log trial distance	0.61 (0.13)	4.56
Block MC	-0.71 (0.14)	-5.20
Block Volatile	-0.14 (0.14)	-1.00
Block MI	-0.10 (0.14)	-0.75
log trial distance × Block MC	0.38 (0.19)	1.99
log trial distance × Block Volatile	0.29 (0.19)	1.51
log trial distance × Block MI	-0.10 (0.19)	-0.50

Discussion

We introduced a novel method to quantify temporal variations in control, by extending the CSE to more remote trials and computing the effects of previous trials on the current trial as a function of trial distance. The rate at which these effects decrease with trial distance was taken as a measure of the time scale of control, with a more gradual decline reflecting a longer time scale.

We observed a longer time scale in the MI block than in the MC block, suggesting a more sustained control mode when conflict is frequent. This is in agreement with models assuming that cognitive control is relatively more affected by recent events when conflict is infrequent (i.e., transient control) and relatively more by remote events when conflict is frequent (i.e., sustained control; Botvinick et al., 2001; De Pisapia & Braver, 2006). These models generally explain differences in control modes by adjustments in time scale parameters, implying that control becomes sustained when conflict is frequent, leaving less room for trial-by-trial variations. The method we introduced here provides a direct empirical measure of this mechanism.

Compared to the MC block, the neutral block also showed a longer time scale of control, but no difference was found between the neutral and MI block. These findings suggest that differences in control modes between MC and MI blocks are due to a switch to a shorter time scale in the MC block rather than to a longer time scale in the MI block. This is in contrast with the suggestion that cognitive control over short time scales is the default mode (Braver, Gray, & Burgess, 2007). However, it is in agreement with the finding that participants decrease their control in response to a cue that indicates that the next block will be MC but do not increase their control when cued with an upcoming MI block (Bugg et al., 2015). Furthermore, some authors have claimed that the relaxation of control after a congruent trial drives the CSE more than the strengthening of control after an incongruent trial (Lamers & Roelofs, 2011; Schlaghecken & Martini, 2011), which also suggests that at least for some tasks, sustained control is the default mode which is abandoned in situations where congruent trials dominate and conflict is rare.

A smaller time scale was also found for volatile compared to MI blocks. This can be explained by a lower conflict frequency in the volatile (i.e., 50%) than in the MI block (i.e., 80%). A trend towards a smaller time scale in the volatile block compared to the neutral block was also present. The volatile block is identical to the neutral block with regard to block-wide conflict frequency, as also confirmed by the similar subjective evaluation of both blocks. However, the changing proportion congruency creates an instable environment which may cause a bias towards more recent information over remote information (Behrens et al., 2007; Jiang et al., 2014).

With regard to the conventional analyses, the overall pattern of CSEs mirrors that of the time scales. Larger CSEs in MC and volatile blocks compared to MI and neutral blocks were found, matching the shorter time scales in MC and volatile blocks. Although this CSE pattern suggests that trial-by-trial adaptations are smaller when conflict is frequent or the environment is predictable, it does not reveal how conflict on recent and remote trials is weighted to influence current conflict processing. For example, there may be conditions where the effect of recent conflict on the current trial is similar (i.e., equal CSEs between conditions), yet differences emerge in the effects of more remote trials. Our time scale approach confirms that there is indeed a larger effect of recent trials in MC and neutral blocks but highlights that this effect decays rapidly with increasing trial distance, resulting in smaller time scales of control.

Apart from our proportion congruency and volatility manipulations, several other factors are likely to elicit different time scales of cognitive control. One factor (or individual difference) that has often be linked to differences in control mode is working memory capacity (e.g., Gulbinaite & Johnson, 2013; Meier & Kane, 2012; Unsworth, Redick, Spillers, & Brewer, 2012). Also, clinical conditions known to affect cognitive control, such as attentional disorders (Nigg, 2005) and schizophrenia (Lesh, Niendam, Minzenberg, & Carter, 2011), may exhibit difficulties with adopting appropriate time scales in different contexts. Finally, our method may also shed new light on the controversy about feature repetition and cognitive control accounts of the CSE. For example, it is unclear whether the repetition account can also explain why time scales would differ across conditions, as shown in the current study, whereas such differences are natural from a cognitive control perspective.

In conclusion, we have successfully applied a novel method to identify the time scale of cognitive control. Smaller time scales of control were demonstrated when conflict was rare and when the context was volatile. This is in line with theories assuming transient control (i.e., control over a shorter time scale) in rare-conflict and volatile conditions, and sustained control (i.e., control over longer time scales) when conflict is more frequent. The method offers promising and straightforward opportunities to quantify variations in the time scale of control between individuals and conditions.

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3

Context-dependent modulation of cognitive control involves different temporal profiles of fronto-parietal activity

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Abstract

To efficiently deal with quickly changing task demands, we often need to organize our behavior on different time scales. For example, to ignore irrelevant and select relevant information, cognitive control might be applied in reactive (short time scale) or proactive (long time scale) mode. These two control modes play a pivotal role in cognitive-neuroscientific theorizing but the temporal dissociation of the underlying neural mechanisms is not well established empirically. In this fMRI study, a cognitive control task was administered in contexts with mainly congruent (MC) and mainly incongruent (MI) trials to induce reactive and proactive control, respectively. Based on behavioral profiles, we expected cognitive control in the MC context to be characterized by transient activity (measured on-trial) in task-relevant areas. In the MI context, cognitive control was expected to be reflected in sustained activity (measured in the intertrial interval) in similar or different areas. Results show that in the MC context, on-trial transient activity (incongruent – congruent trials) was increased in fronto-parietal areas, compared to the MI context. These areas included dorsolateral prefrontal cortex (dlPFC) and intraparietal sulcus (IPS). In the MI context, sustained activity in similar fronto-parietal areas during the intertrial interval was increased, compared to the MC context. These results illuminate how context-dependent reactive and proactive control subtend the same brain areas but operate on different time scales.

Keywords

Attention, Cognitive effort, fMRI, Proportion congruency, Proactive control, Reactive control

Introduction

When our GPS and the road signs point us in opposite directions, we need to overcome automatic tendencies (e.g., adhering to an outdated GPS) in favor of more appropriate responses (e.g., following the road signs). Exerting such cognitive control is crucial in everyday life but also cognitively demanding (Kool, McGuire, Rosen, & Botvinick, 2010; Shenhav et al., 2017; Vassena et al., 2014; Verguts, Vassena, & Silvetti, 2015). Adaptive allocation of cognitive control therefore requires a balance between exerting a sufficient amount (to solve hard tasks), but not too much (to spare costly cognitive effort). As a result, cognitive control is best applied sparsely and should only be sustained when it is frequently needed (Botvinick et al. 2001; Ridderinkhof 2002; Braver et al. 2007; Braver 2012; Jiang et al. 2014).

One way to minimize cognitive expenses while maintaining acceptable performance levels is by applying cognitive control on different time scales. This is mirrored in the way incongruent (i.e., difficult) trials are handled in typical cognitive control tasks. Examples of incongruency can be found in the Stroop task (Stroop, 1935), where word color must be ignored in favor of word meaning, and in the flanker task (Eriksen & Eriksen, 1974), where one should respond to the central target and ignore the flankers. When incongruent trials are rare, reactive control is thought to be active, meaning that control operates in a just-in-time regime (short time scale). Reactive control is thought to be implemented by transient reactivation of task-relevant brain areas (Braver, 2012; Bugg & Crump, 2012; Logan & Zbrodoff, 1979). On tasks with mainly incongruent trials, this transient strategy could lead to frequent errors and delays. Here, a proactive control mode is optimal, operating on a long time scale.

It has been proposed that the brain regions activated during proactive control show anatomical or functional overlap with those activated during reactive control. For example, similar or closely related regions in lateral PFC have been suggested to be involved in reactive and proactive control depending on the specifics of task demands (Braver, 2012; De Pisapia & Braver, 2006). First preliminary support for this context-dependent two-mode (i.e., reactive and proactive) theory of cognitive control came from studies that compared cognitive control between mainly congruent (MC) and mainly incongruent (MI) contexts. In MC contexts, transient (e.g., on-trial) activity in dorsal anterior cingulate cortex (dACC) and other fronto-parietal areas is typically higher on incongruent than on congruent trials (Carter et al., 2000; De Pisapia & Braver, 2006; Grandjean et al., 2012; Jaspar et al., 2016). This is taken as an instance of reactive control and results in slow response times (RTs) and low accuracy on incongruent compared to congruent trials. In MI contexts, the same areas are often found to be activated but the difference between incongruent and congruent trials is less strong or even absent (Carter et al., 2000; De Pisapia & Braver, 2006; Grandjean et al., 2012; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016). This is interpreted as an indicator of sustained control across all trials (congruent and incongruent) in proactive control mode, reducing or eliminating neural and behavioral differences between trial types.

Another way of indexing time scale differences in cognitive control is through hybrid fMRI designs that combine block- and event-related responses (Petersen & Dubis, 2012; Visscher et al., 2003). Here, reactive control is indexed by transient activity on the trial level and proactive control by sustained activity on the block level. Using these designs, the same fronto-parietal areas have been found active in transient and sustained manners, depending on whether the context was MC or MI (Braver et al., 2003; Marini et al., 2016). However, similar designs have also led to claims that two control modes indeed exist but that they not only differ in temporal activation profile but also comprise different brain areas (e.g., Olsen et al., 2010; Seeley et al., 2007). For example, Dosenbach and colleagues (2008) suggested that transient adjustments in control are initiated by a fronto-parietal network including lateral prefrontal and superior parietal cortices. Sustained control, on the other hand, was supported by a cingulo-opercular network comprising dACC and the anterior insula. Consistent with this dual-network perspective on cognitive control, Wilk, Ezekiel, and Morton (2012) also showed that transient and sustained activity can arise from different brain areas. However, in this case, the dACC, anterior insula, and inferior parietal cortex showed transient activity, while sustained activity was found in medial superior frontal gyrus.

In the current study, we adapted the event-related fMRI paradigm to investigate time scale differences in cognitive control. Typically, event-related paradigms measure on-trial activation and are therefore informative about transient, but not sustained activation. To address this issue, we used activity measured in intertrial intervals as a proxy for sustained activation to identify how cognitive control operates in contexts with mainly congruent or mainly incongruent trials. Thus, “active” flanker trials were interleaved with “blank” trials that consisted of a prolonged fixation cross, which allowed measuring context-dependent intertrial activation (Horga et al., 2011). This method offers a novel perspective on two-mode theories about cognitive control and tests whether cognitive control can indeed be allocated with different temporal profiles (reactively and proactively) depending on the context (MC or MI), and whether this involves similar or different brain areas. The blank trials have the additional advantage that they allow measuring activation independent of differences in stimulus-response contingencies, trial difficulty, motor response, accuracy, or response time (Grinband et al., 2011; Schmidt & Besner, 2008).

If context-dependent cognitive control is indeed differently implemented through transient and sustained neural activation, then two neural patterns can be predicted. First, increased on-trial (i.e., transient) activity in typical cognitive control areas, such as dorsolateral prefrontal cortex (dlPFC), dACC, and parietal cortices (Corbetta & Shulman, 2002; Dosenbach et al., 2008; Niendam et al., 2012) is expected on incongruent compared to congruent trials in the MC block but not in the MI block. Second, increased blank-trial activation is expected in the MI block compared to the MC block, reflecting the sustained recruitment of cognitive control in the MI block. Transient and sustained control activation might be located in similar (Braver, 2012; Kerns et al., 2004; Marini et al., 2016) or different (Dosenbach et al., 2008; Olsen et al., 2010; Wilk et al., 2012) brain areas. To complement these hypotheses, we also explored how control-related areas are functionally interconnected in both cognitive control modes, and how they are connected to other (lower-level) areas (Supplemental Material).

Materials and Methods

Participants

Twenty-one healthy native Dutch-speaking participants gave written informed consent to participate. The study was approved by the ethics committee of the Ghent University Hospital. All participants reported no history of psychiatric or neurological disorder, were right-handed, had normal or corrected-to-normal vision, and were rewarded with 30 Euros in exchange for their participation. In addition, a 25 Euros gift coupon was awarded to the best performing participant (as measured by a combined index of RT and accuracy), to increase motivation. One participant was excluded from the analysis because of a technical failure, leaving twenty participants included for statistical analysis (13 females, 7 males, *M* age = 23.32, *SD* = 2.29, age range = 21–28).

Behavioral Task

Participants performed a numerical Eriksen flanker task with the numbers 1, 2, 3, and 4. Stimuli consisted of a central target number, flanked by four identical distractor numbers on both sides (e.g., 11311; see Figure 1a). Participants were instructed to respond to the central target number accurately and as fast as possible by pressing the corresponding button with their left middle finger (1), left index finger (2), right index finger (3), or right middle finger (4). Stimuli (3° wide and 1° high) were displayed until response in black against a grey background and separated by a pseudo-exponential intertrial interval of 1200 to 7200 ms (average = 3000 ms) during which a black fixation cross was displayed centrally. Two different trial types were presented, namely active and blank trials. Active trials could be congruent (i.e., trials with identical target and flankers, e.g., 11111) or incongruent (i.e., trials with different target and flankers, e.g., 11211). All combinations of target and flanker numbers appeared with equal probability on incongruent trials. During blank trials, the fixation cross was presented on screen for 700 ms after the intertrial interval (i.e., a fixation cross remained on screen for an additional 700 ms and no flanker trial was shown). Importantly, because active and blank trials were separated by a jittered intertrial interval, activation on blank trials could be differentiated from activation on the preceding active trials. To the subject, the blank trials did not differ from regular intertrial intervals, since both consisted of a fixation cross.

Procedure

The experiment consisted of a prescanning training outside the scanner and the main session inside the scanner. The whole experiment took about 1 hour 15 min.

Main experiment

Two types of blocks of 68 trials each were presented, with different proportions of congruent trials (see Figure 1a). In the MC block, 48 trials were congruent, 12 were incongruent, and eight were blank, resulting in a congruent:incongruent ratio of 80:20. This ratio was reversed in the MI block with 12 congruent, 48 incongruent and eight blank trials (Horga et al., 2011). Participants were not informed about the occurrence of blank trials but were told that the duration of the fixation cross could vary across trials and that they should stay focused during these intervals. Four MC and four MI blocks were created, resulting in eight blocks that were presented in random order. The task was administered in two consecutive runs with four blocks each. Each block was preceded by a 30s break period.

Trial presentation within a block was random with two constraints. First, in each block, blanks were equally often preceded by a congruent trial and an incongruent trial. Second, each block started with four items representative for the block type (e.g., four congruent items in the MC block). This served to induce the appropriate cognitive control mode at the beginning of the block, to optimize effects on early occurring blanks in that block. For the same reason, participants were cued whether the upcoming block would be MC or MI. The difference between the block types was taught in a separate training session outside the scanner before the start of the experiment (see below), which also served as a practice session. Another ten practice trials were presented inside the scanner before the main experiment to make participants acquainted with the experimental setting.

Prescanning training

The prescanning training had two goals: 1) to familiarize participants with the task and the stimulus-response mappings, and 2) to make participants understand the difference between MC and MI blocks. Participants performed several blocks of 50% congruent practice trials with accuracy feedback. Practice ended as soon as the participant completed a block of 20 trials with 80% accuracy. Next, participants received verbal explanation on the difference between congruent and incongruent trials. To the participants, congruent trials were labelled “identical” and incongruent trials “conflicting” to avoid the rather abstract labels “congruent” and “incongruent”. After that, participants performed several 20-trial MC and MI blocks and were asked to identify each block as MC (i.e., "mostly identical trials") or MI (i.e., "mostly conflicting trials"). This procedure was terminated after the correct identification of four consecutive blocks.

Behavioral data analyses

Two-by-two repeated-measures analyses of variance (ANOVA) with the factors Block Type (MC, MI) and Congruency (congruent, incongruent) were used to analyze the median RT and mean error rate of all trials and trials following blank trials. The following trials were excluded for the RT analysis: trials with RTs faster than 250 ms (0 %) or slower than 2500 ms (1.7 %), error trials (1.9 %) and trials following errors (1.9 %).

fMRI Acquisition

Images were collected by means of a 3 Tesla Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany), with a 32-channel radiofrequency head coil. Participants perceived stimuli projected onto a screen at the extremity of the magnet bore through a mirror mounted on the head coil. Stimulus presentation was controlled by E-Prime 2.0 (Psychology Software Tools, 2012). First, a high-resolution T1-weighted structural scan (MP-RAGE) was conducted followed by two functional runs using a gradient-echo echo-planar pulse sequence. Functional images consisted of 30 axial slices (4 mm thick; 1 mm skip), with TR = 2 s, TE = 33 ms, and 3.5 × 3.5 × 4.0 mm in-plane resolution.

fMRI Data Analysis

fMRI data pre-processing

The fMRI data were pre-processed and analyzed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/software/spm12). Functional data were corrected for differences in acquisition times between slices for each whole-brain volume, realigned within and across runs, and co-registered with each participant's anatomical scan. The functional data were then segmented and spatially normalized to a standard MNI space (2 mm isotropic voxels). Normalized data was spatially smoothed (6 mm full-width at half-maximum, FWHM) using a Gaussian kernel filter. Six motion parameters were estimated using the Artifact Detection Tool software package (ART; https://www.nitrc.org/projects/artifact_detect). These parameters were used to check for outlier scans, which were identified in the temporal differences series by between-scan differences using the following criteria: Z-threshold: 3.0 mm; scan to scan movement threshold: 0.5 mm; rotation threshold: 0.02 radians. Outliers were omitted from statistical analysis by including a single regressor for each outlier. Finally, using ART, no correlations between motion and experimental design, and between global mean signal and experimental design were identified.

Individual-level analysis

Using a general linear model, blood-oxygenation-level dependent (BOLD) responses for all participants were modelled at each voxel. The single-subject analysis was conducted per run and included regressors for each of the events resulting from the within-subjects design involving Block Type (MC, MI) and Congruency (congruent, incongruent) for active trials (i.e., MC_C, MC_I, MI_C, MI_I) and Block Type (MC, MI) for blank trials (i.e., MC_blank, MI_blank), leading to a total of six regressors of interest. In addition, regressors for cues, errors, and previous errors were included as regressors of non-interest. The six motion parameters and outlier regressors identified with ART were included as nuisance regressors. All regressors were time-locked at the onset of the trial. Active and blank trials were analyzed in one model with different basis functions that each capitalized on the properties of the active and the blank trials, thus maximizing statistical power. The active trials were convolved with the canonical hemodynamic response function (HRF) and its time derivative, while the blank trials were convolved with a finite impulse response (FIR) function. The canonical HRF keeps estimator variability low at the cost of some bias, compared to the FIR function. The FIR model was chosen for blanks because of the atypical (non-task) nature of the trials. This strategy allowed for more flexibility to capture the hemodynamic response function (i.e., less bias), at the cost of increased estimator variability (Poldrack, Mumford, & Nichols, 2011). The FIR was estimated across 12 time points, 2 s apart (i.e., the TR), starting at the event onset and ending 22 s later. A high-pass filter of 0.008 Hz was applied and temporal autocorrelations were accounted for using the default first order auto-regressive, or AR(1), model.

Importantly, since all (i.e., active *and* blank) trials were preceded by a jittered intertrial interval, correlations between active and blank trials were kept low. Indeed, the average correlation between active and blank trial regressors was 0.01 (range: -0.19 - 0.21).

Group-level analysis of active trials

One-sample *t*-contrasts for the active trials (i.e., MC_C, MC_I, MI_C, and MI_I) averaged over both runs were taken to a second-level random effects model. We first checked for differences between blocks ([MI_I + MI_C] > [MC_I + MC_C]) and congruency levels ([MC_I + MI_I] > [MC_C + MI_C). To assess which areas are active during cognitive control in the MC block, we next contrasted incongruent and congruent trials in MC blocks (i.e., MC_I > MC_C). The same events were contrasted in the MI block (i.e., MI_I > MI_C). These two analyses were in turn contrasted (i.e., [MC_I > MC_C] > [MI_I > MI_C]) to test for differences in transient activity in the MC versus the MI block. This contrast indirectly tests the prediction that cognitive control in the MI block is characterized by proactive or sustained control across all trials, leading to smaller or absent differences in transient activation between incongruent and congruent trials in the MI block.

Comparisons of interest were tested using two-sample *t*-tests on the group level. Results are reported at a voxel-based threshold corrected for familywise error of multiple comparisons (FWE voxel-wise correction, i.e., $p_{FWE} < 0.05$). In addition, we imposed a minimum cluster extent of 10 voxels. For visualization of results, statistical maps were projected onto a cortical surface with the use of Surf Ice (https://www.nitrc.org/projects/surfice).

Group-level analysis of blank trials

First, functional ROIs were created using the MarsBar toolbox (http://marsbar.sourceforge.net/) based on the outcome of the group-level analyses of the active trials. These ROIs involved a sphere of 8 mm radius around the group-level coordinates of the peak activity of contrast MC_I > MC_C. To assess the second hypothesis that areas that are transiently activated in MC blocks are also active in a sustained way in MI blocks, we compared ROI activity between blanks on MI and MC blocks (i.e., MI_blank > MC_blank). This comparison tests the prediction that task-relevant activation returns to baseline between trials in the MC block but remains high throughout the MI block. Note that this ROI analysis is performed on different trial types than the active-trial analysis (i.e., blanks). Moreover, the contrast of interest is opposite to the one that provided the ROIs, thus precluding double dipping.

FIR functions were averaged across voxels and runs within the ROIs for each participant. Cluster-based non-parametric permutation tests were used for testing the averaged FIR regressor estimates (beta's) for the contrast MI_blank > MC_blank (Maris & Oostenveld, 2007). This method controls for multiple testing (i.e., the FIRs must be compared at 12 different time-points) by taking into account the temporal structure of the data (i.e., the fact that the 12 bins are not independent but have a temporal dependence structure). It allows to investigate the full FIR model, while controlling for multiple testing and without pre-specifying the temporal locus of effect. First, paired sample *t*-tests were performed comparing the regressor estimates at each timepoint between MI and MC blocks. The absolute *t*-values of adjacent timepoints that exceeded the critical *t*-value for a two-tailed *t*-test with 19 degrees of freedom (i.e., $t < -2.09$ and $t > 2.09$) were summed to a maximum observed cluster-*t*. Second, this procedure was repeated after randomly permuting the condition labels (i.e., "MC" and "MI") of each participant 10,000 times, resulting in a null distribution of permutation maximum cluster-*t*'s. Finally, a *p*-value was obtained by testing the observed cluster-*t* against the null distribution. Statistical significance was inferred when the observed cluster-*t* exceeded the 95th percentile of this null distribution.

In addition, we also explored blank-trial activation on the whole-brain level. To restrict the number of tested time bins, we calculated blank-trial activation in five time bins ranging from 4 to 12 seconds after blank onset (i.e., bins 3 to 7). Next, we compared blank-trial activation between MI and MC blocks in each of the five time bins individually. These results were obtained with at a voxel-based threshold corrected for FWE of multiple comparisons (voxel-wise correction, i.e., $p_{FWE} < 0.05$). In addition, a minimum cluster extent of 10 voxels was imposed.

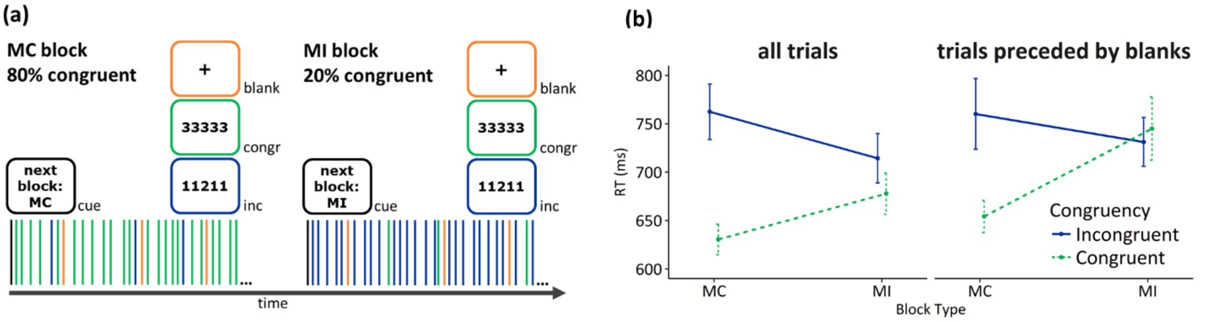

Figure 3. (a) Design of the main experiment. *(b)* Mean of the median response times as a function of Block Type and Congruency for all active trials (left) and only the active trial preceded by a blank (right). MC = mainly congruent, MI = mainly incongruent. Error bars represent standard errors. *** p <0.001, ** p <0.01.

Results

Behavioral results

A repeated-measures ANOVA was conducted on RTs with the within-subject factors Block Type (MC, MI) and Congruency (congruent, incongruent). Effects are displayed in Figure 1b. The results showed a main effect of Congruency, $F(1, 19) = 87.78$, $p < 0.001$, but not of Block Type, $F(1, 19) < 0.01$, $p = 0.98$. Responses were slower on incongruent trials (738 ms) than on congruent trials (654 ms), indicating a congruency effect (CE). A proportion congruency effect (PCE) was also found, as evidenced by the interaction between Block Type and Congruency, $F(1, 19) = 22.01$, $p < 0.001$. The CE was larger in the MC block (132 ms) than in the MI block (37 ms), showing a behavioral dissociation between reactive and proactive control. Similar effects were obtained when the analysis was restricted to the trials preceded by blanks. A main effect of Congruency was found $F(1, 19) = 12.06$, $p = 0.003$, but not of Block Type, $F(1, 19) = 2.56$, $p = 0.13$. Block Type and Congruency also interacted (i.e., a PCE), $F(1, 19) = 11.03$, $p = 0.004$ (see Figure 1b).

A similar repeated measures ANOVA was conducted on error rates. Overall, participants committed few errors (1.9 %). The ANOVA revealed a main effect of Block Type, $F(1, 19) = 12.28$, $p = 0.002$, with larger error rates on MC blocks (2.4 %) than on MI blocks (1.5 %), and a main effect of Congruency, $F(1, 19) = 9.31$, $p = 0.002$, with more errors on incongruent trials (2.6 %) than on congruent trials (1.4 %). No interaction between Block Type and Congruency was found, $F(1, 19) = 0.28$, $p = 0.60$. Analyses restricted to trials preceded by blanks showed a marginally significant main effect of Block Type, $F(1, 19) = 4.13$, $p = 0.056$, with larger error rates on MC blocks (2.4 %) than on MI blocks (0.9 %). No effect of Congruency, $F(1, 19) = 1.64$, $p = 0.22$ was found, nor an interaction between Block Type and Congruency, $F(1, 19) = 0.12$, $p = 0.73$.

fMRI results

Larger transient activity on active trials during reactive control

First, main effects of Block Type and Congruency were assessed. Comparison of the two block types (MI > MC), independent of congruency, yielded no significant activation. Comparison of incongruent and congruent trials, independent of Block Type, revealed larger activation of intraparietal sulcus during incongruent trials (i.e., a general congruency effect; Table 1).

Next, incongruent and congruent trial activation was compared within each block type (MC and MI). It was hypothesized that incongruent trials elicit stronger transient activation in cognitive control areas in the MC blocks (i.e., on MC_I > MC_C). Accordingly, activation was observed in a network of fronto-parietal areas, including the bilateral intraparietal sulcus (IPS), the left inferior frontal gyrus (IFG), the bilateral middle frontal gyrus (MFG), the right dlPFC, and the left pre-supplementary motor area (pre-SMA; see Table 1 and Figure 2a). Contrasting incongruent and congruent trials in the MI block (MI_I > MI_C) was expected to reveal smaller or no transient activation compared to the same contrast in the MC block. Indeed, no voxels survived the statistical threshold in this contrast.

To ensure that the obtained effects reflect differences in cognitive control mode and are not due to a difference in surprise, we also compared congruent trials to incongruent trials in the MI block. Note that congruent trials in MI blocks are equally surprising as incongruent trials in MC blocks. However, cognitive control is only expected to be activated on incongruent trials in the MC block. This contrast (MI_C > MI_I) revealed no activation, ruling out surprise effects.

Finally, cognitive control in MC and MI block was compared directly (i.e., [MC_I > MC_C] > [MI_I > MI_C]). This contrast revealed stronger activation on the MC block in areas identified above, including the bilateral IPS, left IFG, and left MFG (Table 2 and Figure 2b). The reversed contrast (i.e., [MI_I > MI_C] > [MC_I > MC_C]) did not reveal any activation. This suggest that on a transient level, the fronto-parietal network that gets activated during the MC block is less extensively activated during the MI block.

Table 1. *Peak voxel activation in incongruent (minus congruent) trials (i.e., the general congruency effect, I > C) across MC and MI blocks and in the MC and MI blocks separately.*

					MNI coordinates		
Region	**Side**	**Cluster size**	***Z*-score**	***p*(FWE)**	**X**	**Y**	**Z**
MC and MI blocks							
Intraparietal sulcus	R	220	6.30	<0.001	28	-64	54
Intraparietal sulcus	L	305	5.73	0.002	-24	-58	46
MC block							
Intraparietal sulcus	R	1755	>8.00	<0.001	28	-64	56
Intraparietal sulcus	L	2317	7.55	<0.001	-24	-58	44
Inferior frontal gyrus	L	487	7.22	<0.001	-36	6	30
Middle frontal gyrus	R	97	6.13	<0.001	26	6	56
Inferior temporal sulcus	R	53	6.04	<0.001	52	-54	-12
Middle frontal gyrus	L	94	5.93	<0.001	-28	4	52
Cerebellum	R	19	5.42	0.003	26	-62	-28
Middle frontal gyrus (dorsolateral prefrontal cortex)	R	21	5.23	0.008	48	40	26
Pre-supplementary motor area	L/R	26	5.17	0.010	0	10	52
Inferior temporal sulcus	L	13	5.13	0.012	-44	-56	-10
MI block							
None							

Table 2. *Peak voxel activation on incongruent (minus congruent) trials in the MC blocks contrasted with incongruent (minus congruent) trials in the MI blocks.*

					MNI coordinates		
Region	**Side**	**Cluster size**	***Z*-score**	***p*(FWE)**	**X**	**Y**	**Z**
Intraparietal sulcus	R	283	6.30	<0.001	28	-64	56
Intraparietal sulcus	L	931	6.23	<0.001	-32	-48	42
Inferior frontal gyrus	L	164	6.20	<0.001	-38	6	28
Middle frontal gyrus	L	25	5.77	0.001	-28	6	52
Inferior temporal sulcus	L	57	5.66	0.001	-48	-56	-12
Inferior temporal sulcus	R	35	5.60	0.001	50	-52	-12

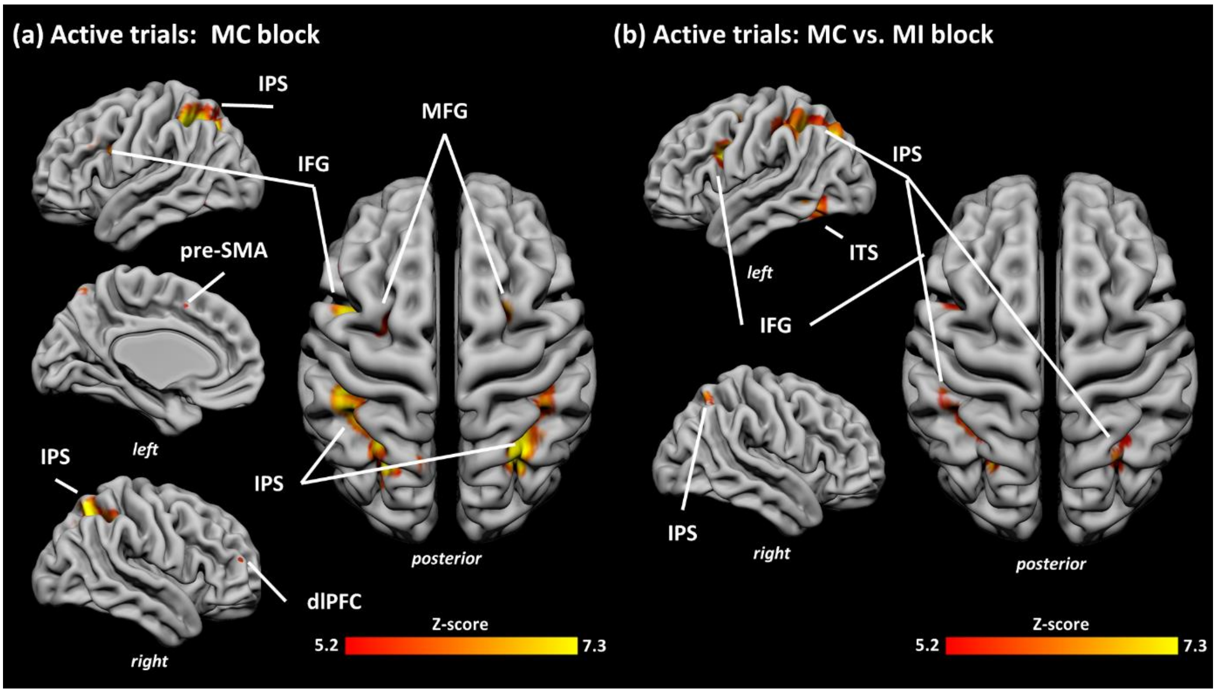

Figure 2. (a) Brain activation on incongruent (minus congruent) trials in the MC block (i.e., MC_I > MC_C). *(b)* Brain activation on the MC block compared to the MI block (i.e., [MC_I > MC_C] > [MI_I > MI _C]). Whole-brain contrasts thresholded at $p_{FWE} < 0.05$ (FWE-corrected). A minimum cluster size of 10 voxels was additionally imposed.

Increased sustained control on blank trials during proactive control

Blank-trial activation was compared between MI and MC blocks (i.e., MI_blank > MC_blank) to test whether control in the MI block involves sustained activity in the same areas that were transiently activated in the MC block. Functional ROIs were obtained from the cognitive control contrast in the MC block from the active-trial analyses (i.e., MC_I > MC_C). The selection was limited to frontoparietal regions commonly associated to cognitive control (Braver, 2012; Corbetta & Shulman, 2002; Dosenbach et al., 2008; Nee, Kastner, & Brown, 2011; Niendam et al., 2012), in this case bilateral IPS, left IFG, bilateral MFG, right dlPFC, and left pre-SMA. The FIR functions displayed in Figure 3 show larger activation on blank trials in MI blocks than in MC blocks at 8-10 s in the bilateral IPS, $p = 0.036$, bilateral MFG, $p = 0.026$ and the right dlPFC, $p = 0.042$. This demonstrates that in these areas, control is exerted via increased activation between trials, in anticipation of a potentially incongruent trial.

In addition, we explored blank-trial activation on the whole-brain level. Blank-trial activity averaged across time bins 3 to 7 (i.e., 4 to 12 seconds post blank-onset) revealed no activation in either direction (i.e., MI_blank > MC_blank or MC_blank > MI_blank). Contrasting blank activation between MI and MC blocks on each of the five time bins individually also did not show activation in either direction.

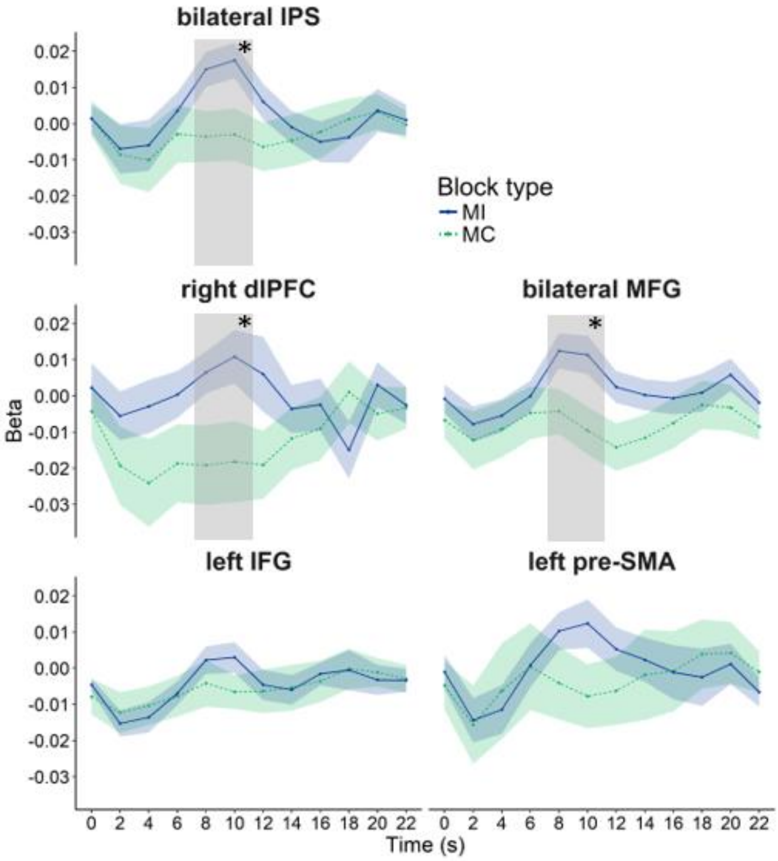

Figure 3. Finite Impulse Response (FIR) functions showing activation during blank trials in MI and MC blocks. * *p* <0.05.

Discussion

Using a paradigm that allowed differentiation of on-trial and intertrial (i.e., blank) activation, we showed a temporal dissociation in cognitive control, depending on the proportion congruency context (MC or MI). A fronto-parietal network comprising the bilateral IPS, left IFG, bilateral MFG, left pre-SMA, and right dlPFC showed increased transient activity on active trials in MC blocks, demonstrating the transient or reactive nature of cognitive control in this context. Conversely, activity was increased in IPS, MFG, and dlPFC during blank trials in the MI block, signaling the sustained or proactive nature of cognitive control in this context. This dissociation shows that reactive and proactive control involve similar brain regions but have different temporal profiles.

Reactive control is mirrored in transient engagement of task-relevant areas

Several frameworks predict that cognitive control can operate on different time scales. For example, enhanced transient cortical responses are proposed to signify the dominance of reactive over proactive control on a given trial (Braver, 2012). In agreement with this, we found increased brain activity on rare incongruent trials in MC contexts, compared to frequent incongruent trials in MI contexts, attesting to the existence of a transient control mode, or reactive control.

Activated areas included the bilateral IPS and right dlPFC, two key areas of the fronto-parietal attention network (Corbetta & Shulman, 2002). Both areas have a well-established role in control of attention (Corbetta & Shulman, 2002; Niendam et al., 2012; Zhang, Geng, & Lee, 2017) and play a central role in cognitive control (Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000), for example through representation of task goals or stimulus-response rules in dlPFC (Braver, 2012; Cole & Schneider, 2007; Corbetta & Shulman, 2002). Increased activation was also found in frontal gyri (IFG, MFG) known to be involved in orienting attention (Marini et al., 2016; Walsh, Buonocore, Carter, & Mangun, 2011; Zhang et al., 2017), and pre-SMA, a region extensively linked to detection and resolution of conflict (Horga et al., 2011; Isoda & Hikosaka, 2007; Nachev, Rees, Parton, Kennard, & Husain, 2005).

Together, the active-trial results illuminate a network of brain regions most likely involved in detecting the occasional need for control (pre-SMA), reactivation of the task goal (dlPFC) and attentional orienting to the task-relevant information (parietal, midfrontal areas) on infrequent incongruent flanker trials. Given that this pattern was observed for incongruent trials in the MC context but not the MI context, it appears that the reignition of task-relevant brain areas is stronger when cognitive control is unexpectedly or infrequently required than when it is needed on most trials. This is consistent with previous work that showed increased on-trial cortical responses during reactive control on other cognitive control tasks (e.g., Carter et al., 2000; De Pisapia & Braver, 2006; Grandjean et al., 2012; Jaspar et al., 2016; Marini et al., 2016; Wilk et al., 2012). Also, exploratory connectivity analyses disclosed stronger connectivity between fronto-parietal and mainly occipital areas on active trials when reactive control was recruited in the MC block. This suggests that the rapid reignition of control is mirrored in increased coupling between fronto-parietal (IPS and dlPFC) and visual (occipital) areas. Note that to successfully solve a flanker trial, attention and vision should be oriented to the central target number. Therefore, this connectivity pattern may reflect interplay between attentional engagement and amplification of task-relevant relative to task-irrelevant stimulus features.

Unexpectedly, no incongruency-related dACC activity was found, even though dACC has been extensively linked to cognitive control and/or cognitive effort (Botvinick et al., 2001; Braver, 2012; Cole & Schneider, 2007; De Pisapia & Braver, 2006; Holroyd & Yeung, 2012; Shenhav, Botvinick, & Cohen, 2013; Wilk et al., 2012). Yet, absence of dACC activity is not uncommon when flanker tasks are used to target cognitive control. For example, Marini et al (2016) found no incongruency-related activity in whole-brain analyses, and a meta-analysis of different cognitive control tasks has shown that dACC is not always among the regions typically activated on flanker tasks (Nee, Wager, & Jonides, 2007). It is also relevant to mention that because of their anatomical proximity and often concurrent activation, it can be difficult to distinguish activation of dACC and pre-SMA during cognitive processing (Jahn, Nee, Alexander, & Brown, 2016).

Intertrial activation shows the sustained nature of proactive control

Different transient activation dynamics in fronto-parietal areas on MC and MI contexts do not directly attest to the proactive nature of control in the latter context. The activation during intertrial intervals however does provide support on this matter, by showing that task-relevant areas are more active on blank trials in the MI context than in the MC context. We observed that the same areas that are recruited reactively on active trials in MC contexts (i.e., bilateral IPS, bilateral MFG, and right dlPFC) are more strongly activated on blank trials in MI compared to MC contexts. The fact that the direction of the effect is opposite for active and blank trials and the fact that previous-trial congruency was controlled for, rule out the possibility that blank-trial activation reflects residual activation induced by the previous active trial. In addition, these results were obtained while experimentally controlling for visual stimulation, stimulus-response contingencies, trial difficulty, motor response, accuracy, and response time.

Diminished transient responses to incongruency during the MI context and increased sustained responses between trials in that same context offer an empirical demonstration of the mechanisms involved in reactive and proactive control. As suggested before (De Pisapia & Braver, 2006; Kerns et al., 2004), a large proportion incongruency may lead to a tonic increase of cognitive control-related activity, which in turn reduces the transient neural response to incongruency at the trial level. This also explains the smaller behavioral effect of incongruency in MI contexts.

The brain areas that appear to be involved in this balance of transient and sustained activity included IPS and dlPFC. These areas are part of the fronto-parietal network that serves to initiate and adjust cognitive control (Corbetta & Shulman, 2002; Dosenbach et al., 2008) and encompasses functions such as sustaining representations of the task goal (e.g., “respond to central number”; MacDonald et al. 2000; Miller and Cohen 2001; Braver 2012) and attentional engagement (e.g., narrowing attention to central number; Walsh et al. 2011; Marini et al. 2016). Since dlPFC and IPS were also recruited during reactive control, task goal representation and attentional engagement may be active during both control modes in a qualitatively similar way but, importantly, only transiently when control is occasionally needed during reactive control.

The involvement of similar areas is consistent with findings of hybrid fMRI studies that statistically separated transient and sustained responses to show involvement of similar areas in reactive and proactive control (Braver et al., 2003; Marini et al., 2016). However, other work has shown that transient and sustained control may recruit different areas (e.g., Dosenbach et al., 2008; Wilk et al., 2012). Since the current whole-brain analyses did not show any blank-trial activation, it remains speculative whether context-driven reactive and proactive control are indeed solely bound to similar brain areas and differ only in terms of temporal profiles, or whether they are also partly comprised by different regions.

The fact that sustained activation extended beyond dlPFC to IPS is partly consistent with the work of Dosenbach and colleagues (2008). They suggest that both dlPFC and IPS have a superordinate function in maintenance of task goals and contexts, but on a short time scale (i.e., in the range of a small number of trials), while dACC and anterior insula provide stable task-set maintenance (i.e., in a range that spans all trials in a task epoch (see also Holroyd & Yeung, 2012). The current results partly agree with this dual-networks perspective in the sense that dlPFC and IPS indeed showed transient trial-to-trial adjustments. However, both regions were also activated in a sustained manner. This suggests that dlPFC and IPS are functionally related and can operate transiently, but also on a time scale that spans more than a few trials (i.e., on the block level). Yet, given its extensive involvement in attentional orienting (Corbetta & Shulman, 2002; Marini et al., 2016; Walsh et al., 2011), the role of IPS in top-down control may be qualitatively different from more abstract task-goal maintenance. Inconsistent with Dosenbach and colleagues (2008), we found no activation of dACC or anterior insula on a long time scale. The current contrast-analyses therefore cannot elucidate if and how dACC and anterior insula fit into dual-networks perspectives on cognitive control. However, exploratory connectivity analyses did show increased coupling between IPS and dACC during proactive control. This may signify the involvement of dACC in optimizing cognitive processing in task-specific areas such as IPS, through sustained investment of effort (Holroyd & Mcclure, 2015; Holroyd & Yeung, 2012; Shenhav et al., 2013; Verguts et al., 2015).

Activity-silent cognitive control

The exact implementation of transient and sustained engagement of task-relevant areas in reactive and proactive control remains an open question. A potential explanation may come from working memory studies that have demonstrated that recent information can remain dormant in pre-synaptic (activity-silent) connectivity. When needed, such connectivity may suddenly lead to (metabolically more costly) spiking activity (Mongillo, Barak, & Tsodyks, 2008; Rose et al., 2016; Stokes, 2015). In line with this synaptic working memory theory, we suggest that reactive control in MC contexts involves maintaining task-relevant information in pre-synaptic traces. When a task cue or stimulus is presented (in this case a rare incongruent trial) such traces can be reactivated, leading to a transient rise of fronto-parietal activation and a reconnection of this network with relevant sensory areas.

Further in line with synaptic working memory theory, we suggest that in proactive control mode, task-relevant information remains in active firing mode because it needs to be applied frequently. This has the advantage of being more readily available at all times, but also increases metabolic costs. Sustained control therefore taxes the cognitive system (Braver et al., 2007), and subjects will tend to avoid it to reduce cognitive effort (Kool et al., 2010).

In the current design, sustaining control was necessary to achieve optimal task performance in MI blocks. Subjects could expect the next trial to be incongruent but the occurrence of the next stimulus could not be predicted because of the jittered stimulus presentation. This forced subjects to remain on guard in the intertrial interval in the MI block. Elaborating on synaptic working memory and effort avoidance theories, one would expect this strategy to be abandoned in favor of a more metabolically efficient (i.e., less effortful) strategy when stimulus presentation is temporally predictable. In that case, activity may stay silent throughout most of the interval also in MI blocks, and ramp-up right before stimulus presentation, resulting in a phasic form of proactive control. This prediction remains to be tested.

Conclusion

The current study demonstrates how the brain flexibly implements cognitive control on different time scales, depending on the context. It shows that cognitive control in MC and MI contexts is subtended by different temporal activation of the same fronto-parietal areas. In MC contexts, or reactive control mode, transient activity in task-relevant fronto-parietal areas is larger. In MI contexts, or proactive control mode, sustained activation in similar areas is increased between trials. Together, these results explain how reactive and proactive control recruit similar brain areas but on different time scales.

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Supplemental Material

Functional connectivity analyses

Generalized psychophysiological interactions (gPPIs; Mclaren et al. 2012) were computed to explore how control-related areas are interconnected in both cognitive control modes, and how they are connected to lower-level sensory areas. Seed-to-voxel maps were computed using the CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). Unsmoothed preprocessed images were used for extracting ROI-level average BOLD signal timeseries. BOLD signal was first denoised by implementing aCompCor. This removed possible confounds such as BOLD signal from subject-specific white matter and CSF masks, nuisance regressors created in the individual-level analysis, and main condition effects. Voxels of each ROI were restricted to those voxels within estimated subject-specific grey matter masks. A high-pass filter of 0.008 Hz was used. Generalized psychophysiological interaction (gPPI; Mclaren et al. 2012) analyses were performed with seeds obtained from the (MC_I > MC_C) contrast on the active trials (i.e., bilateral IPS, right dlPFC, left IFG, left IMG, and left pre-SMA). Connectivity patterns with a particular seed were computed on congruent, incongruent, and blank events (for each block type), simultaneously in the gPPI models. Separate models were computed for each individual seed. The resulting seed-to-voxel beta maps were taken to a second-level random effects model to identify voxels that correlated differentially with the seed in an event-dependent matter. For this purpose, one-sample *t*-tests were used on the group level thresholded at voxelwise p <0.001 and cluster-size $p_{\text{FWE}} < 0.05$.

For active trials, connectivity values were compared between the two blocks according to (MC_I > MC_C) > (MI_I > MI _C) to reveal connectivity patterns during transiently applied control. This revealed connectivity between seeds (IPS, MFG, IFG, and dlPFC) and regions that were mostly located in occipital cortex (see Table S1 and Figure S1).

For the blank trials, seed-voxel connectivity was compared between MI and MC blocks to investigate connectivity when control is sustained (proactive control; MI_blank > MC_blank). Increased connectivity was found between IPS and dorsal anterior cingulate cortex (dACC) when proactive control was active in the MI blocks (see Table S1 and Figure S1).

Table S1. *Functional connectivity results. Seeds are in italics.*

Region	**Side**	**Beta**	**Clust. size**	**Clust. size *p*(FWE)**	***Z*-score**	***p*(unc.)**	**MNI coordinates**		
							X	**Y**	**Z**
Active trials									
Bilateral IPS									
Lateral occipital cortex / cuneus	L	0.058	640	<0.001	4.47	<0.001	-20	-96	18
Lateral occipital cortex	R	0.060	672	<0.001	4.39	<0.001	32	-80	22
Superior temporal gyrus	L	0.055	107	<0.001	4.13	<0.001	-50	-32	-2
Cerebellum	R	0.044	75	0.040	4.01	<0.001	42	-64	-30
R dlPFC									
Anterior prefrontal cortex	L	0.049	129	0.001	4.30	<0.001	-26	56	6
Middle temporal gyrus	R	0.057	99	0.006	4.46	<0.001	60	2	-20
L IFG									
Lateral occipital cortex	L	0.050	519	<0.001	4.70	<0.001	-26	-84	-10
Occipital pole	R	0.053	354	<0.001	4.38	<0.001	30	-88	-4
Lateral occipital cortex	R	0.050	114	0.003	4.04	<0.001	32	-88	20
L MFG									
Occipital pole / lateral occipital cortex	L	0.051	99	<0.001	3.92	<0.001	-20	-98	10
Pre-SMA									
None									
Blank trials									
Bilateral IPS									
Dorsal anterior cingulate cortex	R	0.02	77	0.043	4.65	<0.001	-8	30	10

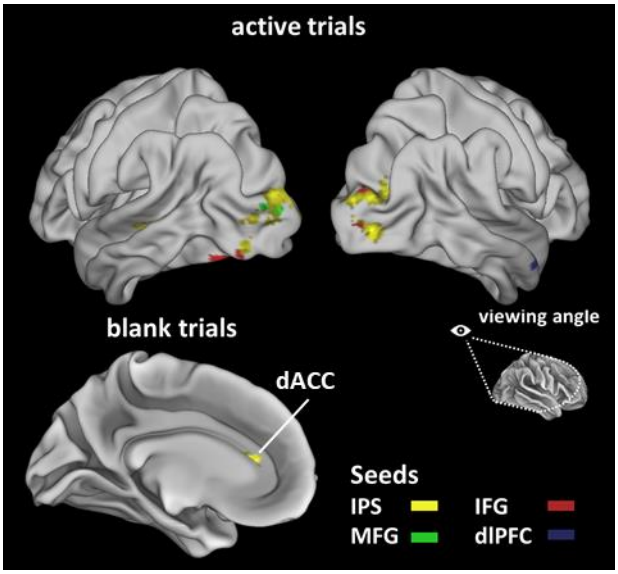

Figure S1. Seed-voxel connectivity computed on active trials through the contrast (MC_I > MC_C) > (MI_I > MI_C) and on blank trials with the contrast MI_blank > MC_blank. Colored areas depict voxels that showed connectivity to the respective seed. dACC = dorsal anterior cingulate cortex, dlPFC = dorsolateral prefrontal cortex, IFG = inferior frontal gyrus, IPS = intraparietal sulcus, MFG = middle frontal gyrus.

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4

Cognitive effort modulates connectivity between dorsal anterior cingulate cortex and task-relevant cortical areas

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Abstract

Investment of cognitive effort is required in everyday life and has received ample attention in recent neurocognitive frameworks. The neural mechanism of effort investment is thought to be structured hierarchically, with dorsal anterior cingulate cortex (dACC) at the highest level, recruiting lower-level task-specific areas. In the current fMRI study, we tested whether dACC is generally active when effort demand is high across different tasks, and whether connectivity between dACC and task-specific areas is increased depending on the task and effort level at hand. For that purpose, two perceptual detection tasks were administered that required male and female human subjects to detect either a face or a house in a noisy image. Effort demand was manipulated by adding little (low effort) or much (high effort) noise to the images. Results showed a network of dACC, anterior insula (AI), and intraparietal sulcus (IPS) to be more active when effort demand was high, independent of the performed task. Importantly, effort demand modulated functional connectivity between dACC and face- or house-responsive perceptual areas, depending on the task at hand. This shows that dACC, AI, and IPS constitute a general effort-responsive network and that the neural implementation of cognitive effort involves dACC-initiated sensitization of task-relevant areas.

Keywords

Cognitive control, Cognitive effort, dACC, Functional connectivity, PPI

Introduction

Cognitive effort plays an important role in many aspects of daily life. For example, its investment can lead to feelings of cognitive fatigue (Boksem & Tops, 2008; Inzlicht, Shenhav, & Olivola, 2018; Müller & Apps, 2019); it is perceived as aversive and therefore avoided if possible (Kool, McGuire, Rosen, & Botvinick, 2010; Kurzban, Duckworth, Kable, & Myers, 2013); and it is registered as a cost in decision making (Apps, Grima, Manohar, & Husain, 2015; Botvinick, Huffstetler, & McGuire, 2009; Shenhav, Botvinick, & Cohen, 2013). Cognitive effort is closely related to, but distinct from, task difficulty. Whereas effort is a property of the actor (i.e., defined as the investment of cognitive resources), difficulty is a property of the task (Inzlicht et al., 2018). For example, a task can be difficult without the actor investing much effort into it.

Cognitive effort can be conceptualized as the amplification of cognitive activity to resolve a demanding cognitive task (Inzlicht et al., 2018). Research on effort-based decision making has identified a network of brain regions that are active when a person engages in effortful behavior. This circuitry mainly involves dorsal anterior cingulate cortex (dACC), anterior insula (AI), lateral prefrontal cortex (lPFC), and intraparietal sulcus (IPS; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Menon & Uddin, 2010; Shenhav et al., 2013). Although dACC and AI in particular are often jointly activated across various tasks (Engström, Karlsson, Landtblom, & Craig, 2015; Medford & Critchley, 2010; Nelson et al., 2010), it is generally thought that dACC is more directly involved in effort allocation. Instead, AI may signal the saliency of events (Menon & Uddin, 2010; Shenhav et al., 2017) or represent task-set maintenance (Dosenbach et al., 2006; Nelson et al., 2010). Therefore, recent frameworks have positioned dACC at the top of a hierarchy, exhibiting increased activity whenever effort demand is high, independent of the task that is performed (Holroyd & Yeung, 2012; Verguts, Vassena, & Silvetti, 2015). To solve a difficult task, it is believed that dACC, as part of a broader network of brain regions, recruits specialized upstream areas such as perceptual regions.

The activation of perceptual areas by top-down processes has been reported previously. For example, dACC is involved in top–down attentional modulation of task-relevant perceptual areas (Crottaz-Herbette & Menon, 2006; Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011). The mere expectation of a face or house image can also be sufficient to evoke activity in fusiform face area (FFA) and parahippocampal place area (PPA), respectively (Esterman & Yantis, 2010; Summerfield, Egner, Mangels, & Hirsch, 2006). In the present fMRI study, we built on these findings to elucidate how effort investment is implemented in the brain and to investigate if dACC indeed recruits specialized lower-level areas when effort demand is high.

In two perceptual detection tasks, subjects decided whether an image contained either a face or a house, or only noise. To disclose the top-down effects of effort investment on perceptual performance, we manipulated the effort required to solve the tasks by adding little (low-effort trials) or much (high-effort trials) noise to the images. With much noise, the perceptual evidence contained by the image is low. On such difficult occasions, additional cognitive effort is required for the actor to reach an accurate decision. We hypothesized that this increased effort may serve as a top-down amplifier of the low signal-to-noise ratio, leading to an improvement in detection accuracy in noisy circumstances (Shenhav et al., 2013; Verguts et al., 2015). Specifically, we expected increased activation of effort-responsive areas such as dACC and AI, when effort demand is high, independent of the task that was performed. Importantly, because participants knew beforehand whether they had to detect a face or a house, we expected that dACC would increase its functional connectivity to FFA and PPA, respectively, when effort-demand was high compared to low. This would show that dACC exerts its effects by modulating upstream areas, when effort investment is large.

Materials and Methods

Participants

Thirty healthy participants gave written informed consent to participate (19 females, 11 males, *M* age = 23.07, *SD* = 3.48, age range 18-33). The study was approved by the ethics committee of the Ghent University Hospital. All participants reported no history of psychiatric or neurological disorder, were right-handed, had normal vision, and were rewarded with 30 Euros in exchange for their participation.

Stimuli

Grayscale images of 18 faces and 18 houses were used (Figure 1; Schiffer, Muller, Yeung, & Waszak, 2014). Several measures were taken to nullify differences in surface properties between images. First, the images were equated in mean luminance level, contrast, and spatial frequency using the SHINE toolbox (Spectrum, Histology and Intensity Normalization and Equalization; Willenbockel et al., 2010).

Next, for each trial, noise masks were created through image phase scrambling. Fast Fourier transforms (FFT) were computed of one randomly selected face image and one randomly selected house image. The amplitude and phase matrices of these images were averaged across the two images. A random phase matrix was added to the averaged phase matrix, resulting in 100% phase scrambling. The final noise mask was obtained through inverse fast Fourier transformation (IFFT) of the averaged amplitude matrix and the averaged phase plus noise matrix.

Two different trial types were created: target-present and target-absent trials. On target-present trials, a face or house image was blended with a noise mask. The blending depended on a threshold corresponding to a participant- and task-specific interpolation factor. These thresholds were obtained from a staircase procedure performed before the main task (see *Staircase procedure*). The thresholds could vary from 0, meaning that the original face or house image was returned, to 1, meaning that the noise mask was returned.

Each target-absent trial consisted of a superimposed face and house image (i.e., they were blended with interpolation factor 0.5). Next, the superimposed image was 100% phase scrambled. This phase-scrambled image was in turn blended with the noise mask, with an interpolation factor that was the average of the face and house threshold obtained from the participant's staircase performance (see below). This procedure assured identical target-absent trials in all conditions.

Experimental Design and Statistical Analysis

Target detection tasks

On each trial, participants were shown a noisy image displayed against a grey background at 6.2° x 8° visual angle (Figure 1B). Two different target detection tasks were administered. In the face task, participants had to decide whether the noisy image contained a face (target present) or not (target absent); in the house task, they had to decide whether the image contained a house or not (Figure 1B). Participants pressed a button either with the right index or middle finger for a target-present or target-absent trial. Response mapping was counterbalanced across participants. Each trial consisted of a 1000-ms image presentation, during which participants were not allowed to respond yet, followed by a 1000-ms response window during which a question mark was displayed, and responses were recorded. Trials were separated by a pseudo-exponentially distributed intertrial interval ranging from 1000 to 7000 ms (average = 3000 ms) during which a fixation cross was displayed.

Each task was performed at two effort levels: In the low-effort condition, the difference in target visibility between target-present and target-absent trials was large; in the high-effort condition this difference was small (Figure 1A). Specifically, the effort level of each block depended on the interpolation level of the target images. In low-effort blocks, the interpolation level of each target image was randomly drawn from a normal distribution centered around 0.30 with *SD* = 0.07. This resulted in a clear difference between target and noise trials (Figure 1A). In high-effort blocks, the interpolation level of target images was randomly drawn from a normal distribution centered around the threshold obtained through a staircase procedure (see *Staircase procedure*), with *SD* = 0.07. Hence, on high-effort blocks, the difference between target and noise images was much smaller (Figure 1A).

Task (face vs. house detection) and Effort (low vs. high) were varied block-wise, resulting in four different block types, or conditions: face low-effort, face high-effort, house low-effort, and house high-effort (Figure 1A). Each block contained 18 trials, half of which were target-present trials while the other half were target-absent trials. Blocks were presented in five rounds, resulting in a total of 90 trials per condition. Each round contained a single presentation of all block types in random order.

Participants were made aware of the difference between low and high-effort blocks through verbal instructions before the experiment started. They were also cued at the start of each block about which task to perform (i.e., detect face or detect house) and whether the block was a low- (i.e., "easy") or high-effort (i.e., "difficult") block (Figure 1B). Participants were instructed to stay focused on the center of the images to avoid eye movements. Accuracy feedback was provided at the end of each block.

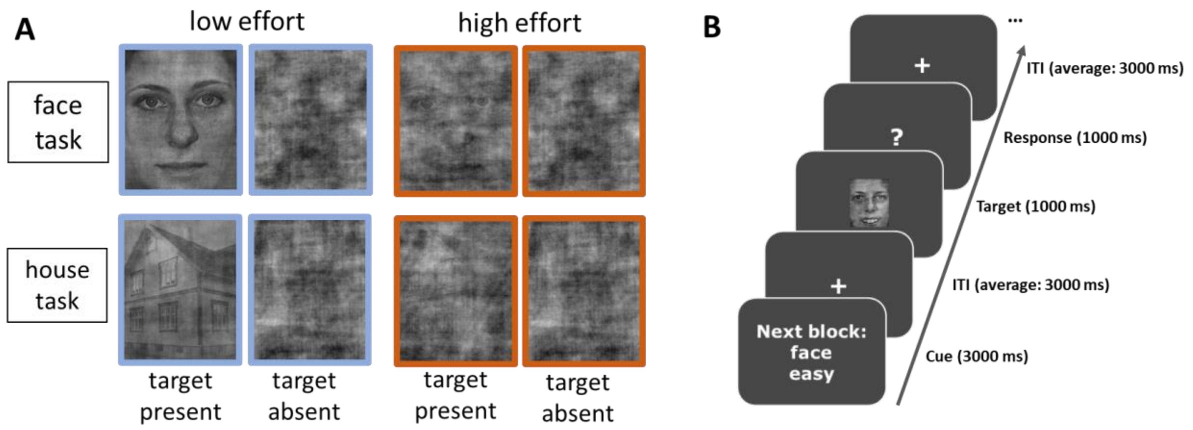

Figure 1. A) Examples of the face and house stimuli in the four conditions. The color coding is used for clarification only and was not used in the experiment. *B)* Paradigm of the target detection tasks. Each block started with a cue signaling the task the subject had to perform: decide if the image contained a face (target present) or not (target absent), or decide if the image contained a house or not. The cue also indicated the effort level of the task ("easy" for low effort, "difficult" for high effort). The trial displayed here is an example of a target-present trial in the low-effort condition of the face-detection task.

Target detection tasks: d' analysis

For each participant and condition (face low-effort, face high-effort, house low-effort, and house high-effort), we computed the d' to evaluate performance. d' is a measure of the difference between the mean sensory activity generated by signal plus noise trials versus noise alone trials, expressed in *Z*-scores. A 2×2 repeated-measures analyses of variance (ANOVA) with the factors Task (face vs. house) and Effort (low effort vs. high effort) was performed on these d' measures. Trials with no response were excluded from analysis (2.9%).

Subjective rating task

To ensure that the high-effort conditions of the target detection tasks were indeed perceived as more difficult than the low-effort conditions and that participants indeed invested more effort into it, a separate sample of 32 first-year psychology students was recruited (27 females, 5 males. *M* age = 18.72, *SD* = 1.30, age range = 18-23). All participants gave written informed consent and were rewarded with one course credit. They were administered the same target-detection tasks described above, outside the scanner, and with the addition of two questions after each block of trials. One question probed task difficulty: "How difficult did you find the previous block?". The other probed invested effort: "How much effort did it take you to complete the previous block?". Participants rated difficulty and effort investment on a horizontal line ranging from 0 ("not difficult at all" or "no effort at all") to 100 ("extremely difficult" or "extreme effort"). The questions were presented in random order after each block.

Subjective rating task analysis

The ratings of difficulty and effort investment were averaged per participant and condition. These ratings were subjected to a repeated-measures ANOVA with the factors Task and Effort.

Staircase procedure

Before the target detection task, participants performed a linear adaptive one-up-two-down staircase outside the scanner to determine the interpolation factor for each participant for the high-effort blocks. This was done in two separate blocks for face and house images. The trial procedure was similar to the main task, except for the inclusion of feedback on accuracy ("correct" and "false") and response time ("too slow" when the response deadline of 1000ms was exceeded). Participants performed two blocks of 72 trials separated by a 10s pause. Based on pilot data, the initial interpolation level was set at 0.65 for each block. The interpolation level dropped with one step after every incorrect response and increased with one step after two consecutive correct responses. For the first four reversals, the step size was set at 0.02, to accelerate progressing through the staircase in the beginning. From the fifth reversal, the step size was set to 0.01. The average interpolation level on the last six reversals was taken as the participant's interpolation factor. The mean interpolation level was 0.80 (*SD* = 0.02, range = 0.71-0.83) for the Face task and 0.77 (*SD* = 0.03, range = 0.70-0.82) for the House task. Block order was counterbalanced between participants. Response configuration was kept identical between the staircase task and the target detection task.

fMRI acquisition

Images were collected by means of a 3 Tesla Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany), with a 64-channel radiofrequency head coil. Participants perceived stimuli projected onto a screen at the extremity of the magnet bore through a mirror mounted on the head coil. Stimulus presentation was controlled by PsychoPy v1.85.4 (Peirce, 2007). First, a high-resolution T_1-weighted structural scan (MP-RAGE) was conducted (176 slices, 1mm slice thickness, TR = 2250ms, TE = 4.18ms, flip angle = 9°). This was followed by two functional runs using a gradient-echo echo-planar pulse sequence. Functional images consisted of 38 axial slices (3.5 mm thick; 1 mm skip, 229 field of view), with TR = 2s, TE = 29ms, flip angle = 90°, and 3.5 × 3.5 × 3.5 mm in-plane resolution.

fMRI data analysis

fMRI data preprocessing

The fMRI data were preprocessed and analyzed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/software/spm12). Functional data were corrected for differences in acquisition times between slices for each whole-brain volume, realigned within runs, and co-registered with each participant's anatomical scan. The functional data were then segmented and spatially normalized to standard MNI space (2 mm isotropic voxels). Normalized data were spatially smoothed (6 mm full-width at half-maximum, FWHM) using a Gaussian kernel filter. Six motion parameters were estimated using the Artifact Detection Tool software package (ART; https://www.nitrc.org/projects/artifact_detect). These parameters were used to check for outlier scans, which were identified in the temporal differences series by assessing between-scan differences using a *Z*-threshold of 5.0 mm and a scan to scan movement threshold of 0.9 mm. The motion parameters and outlier regressors identified with ART were included in all first-level statistical analyses as nuisance regressors.

Target detection task

Using a general linear model (GLM), blood-oxygenation-level dependent (BOLD) responses for all participants were modelled at each voxel. Initially, a hybrid design modeling both transient trial responses and sustained block responses was explored in one design (Petersen & Dubis, 2012; Visscher et al., 2003). However, the block regressors had to be dropped because of high collinearity. The remaining design included four trial types, resulting from the crossing of the factors Task (face vs, house) and Effort (low effort vs. high effort). Trial regressors were convolved with a canonical HRF, including time and dispersive derivatives. The event length was set at 0 seconds. The six motion parameters and outlier regressors identified with ART were included as nuisance regressors. A high-pass filter of 0.008 Hz was applied, and temporal autocorrelations were accounted for using the default first order auto-regressive, or AR(1), model.

We first checked for task-specific effects by computing contrasts between the face and house tasks for low and high-effort conditions. In a similar vein, contrasts were computed between low and high-effort conditions for face and house tasks to identify effort effects. Individual contrast maps were subjected to second-level random effects models. Significance was tested through one-sample *t*-tests. Since FFA activity is generally more robust in right than in left hemisphere in right-handers (Kanwisher, McDermott, & Chun, 1997; Willems, Peelen, & Hagoort, 2010), we also applied a small volume correction in case bilateral activity was not found in whole-brain analyses. Small volume correction was done with 10-mm bilateral spherical ROIs centered at the mean peak-voxels obtained from the localizer. To determine which regions were responsive to high-effort demand across tasks, a conjunction analysis was performed on the two activations maps that compared low versus high effort conditions in the face and the house task. The conjunction null hypothesis was assessed (Nichols, Brett, Andersson, Wager, & Poline, 2005), meaning that only regions significant in both contrasts survived.

Results are reported at an uncorrected voxel-based threshold of $p < 0.001$ and cluster corrected to control the FWE at $p = 0.05$. For visualization of results, statistical maps were projected onto 2D slices using MRIcroGL (https://www.nitrc.org/projects/mricrogl) and on cortical surfaces with the use of Surf Ice (https://www.nitrc.org/projects/surfice).

Functional connectivity

A generalized psychophysiological interaction (gPPI) analysis was conducted to assess whether connectivity between effort-responsive regions (dACC) and lower-level sensory cortices increased in a task-dependent way. This analysis was conducted on unsmoothed volumes with the CONN toolbox (http://www.conn-toolbox.org; Whitfield-Gabrieli & Nieto-Castanon, 2012). To remove non-neural sources from the neural signal, an anatomical component-based noise correction (aCompCor) strategy was used (Behzadi, Restom, Liau, & Liu, 2007). The six realignment parameters were regressed out and the BOLD signals from individual white matter and cerebrospinal fluid (CSF) masks were used to remove noise components. Next, the gPPI model was estimated according to

$$y = \beta_0 + \beta_1 S + \beta_2 FaceLE + \beta_3 FaceHE + \beta_4 HouseLE + \beta_5 HouseHE \\ + \beta_6 FaceLE{\times}\mathrm{S} + \beta_7 FaceHE{\times}\mathrm{S} + \beta_8 HouseLE{\times}\mathrm{S} + \beta_9 HouseHE{\times}\mathrm{S}$$

where *S* is the averaged time series of the seed region; *FaceLE, FaceHE, HouseLE* and *HouseHE* are the psychological (block) regressors representing the four conditions; and *FaceLE×S, FaceHExS, HouseLExS* and *HouseHE×S* are the interactions between the seed's averaged time series and the psychological regressors.

Given that connectivity analyses gain power when events are stretched across longer time periods (Gonzalez-castillo, Hoy, Handwerker, Robinson, & Buchanan, 2015), we utilized the blocked structure of the design for the gPPI analysis, using block regressors. The seed's time series was not deconvolved, given that deconvolution is deemed unnecessary when a blocked design is used (Di & Biswal, 2017; O'Reilly, Woolrich, Behrens, Smith, & Johansen-berg, 2012). The psychological regressors were convolved with the hemodynamic response function and the interactions were modeled on the raw BOLD-level signal.

This analysis was first conducted on whole-brain level, assessing seed-to-voxel connectivity. The individual beta values corresponding to the interaction terms (β_6 to β_9) were subjected to a second-level random effects analysis, where we contrasted low- and high-effort blocks within each task (i.e., FaceHE > FaceLE; HouseHE > HouseLE) and assessed the difference between these two contrasts (i.e., [FaceHE > FaceLE] vs. [HouseHE > HouseLE]).

The whole-brain analysis was followed-up by a ROI-to-ROI analysis, where we estimated the interaction terms (β_6 to β_9) using the averaged time series of individual FFA and PPA target ROIs (see *Localizer*). The interaction terms were first subjected to multivariate *F*-tests to jointly evaluate whether the connectivity between the seed and any of the target ROIs showed any significant effect of interest. This was followed by FDR-corrected individual *t*-tests between the seed and each of the target ROIs.

Localizer

A functional localizer task was administered after the main experiment to identify face- and house-selective areas (i.e., FFA and PPA, respectively). Participants performed a 1-back task where they had to press a button with the right index finger for any immediate repetition of an image. The same face and house images as in the target detection task were presented blockwise in eight 18-trial blocks of each type (16 blocks in total). No noise was added to the images. Face and house blocks alternated. Which block was presented first, was counterbalanced across participants. Image presentation within blocks was random. Images were displayed for 1500ms and separated by a 500ms fixation cross. Mean accuracy on immediate repetitions was 88.8% on face trials and 90.4% on house trials, $t(29) = -0.76$, $p = 0.46$.

Blocks of face and house images were modeled by boxcar functions convolved with the canonical HRF and its time derivative. Lengths of the boxcars corresponded with the block lengths. To obtain individual ROIs, the following procedure was implemented. First, a GLM was created with regressors for Face and House blocks. Individual contrast maps were computed comparing Face vs. House and vice versa, using an uncorrected voxel-based threshold of $p < 0.001$ and cluster correction to control the FWE at $p = 0.05$. Second, FDR-corrected activation maps were obtained from the Neurosynth database (http://www.neurosynth.org; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) using the search terms “fusiform” (n = 972), “fusiform face” (*n* = 143), “fusiform gyrus” (*n* = 91), and “fusiform gyri” (*n* = 582), for FFA, and “parahippocampal” (*n*=602), “parahippocampal cortex” (*n* = 76), and “parahippocampal gyrus” (*n* = 327) for PPA. These maps were binarized and combined into two single activation maps (one for bilateral FFA, one for bilateral PPA). Finally, the intersections between each Neurosynth activation map and the corresponding individual contrast map from the localizer task were computed. Six-mm spheres were created, centered on the peak voxel coordinates within the remaining left and right clusters of the two intersection contrasts (i.e., Face vs. House and

House vs. Face). This resulted in four ROIs for each participant: left FFA, right FFA, left PPA, and right PPA (Figure 2).

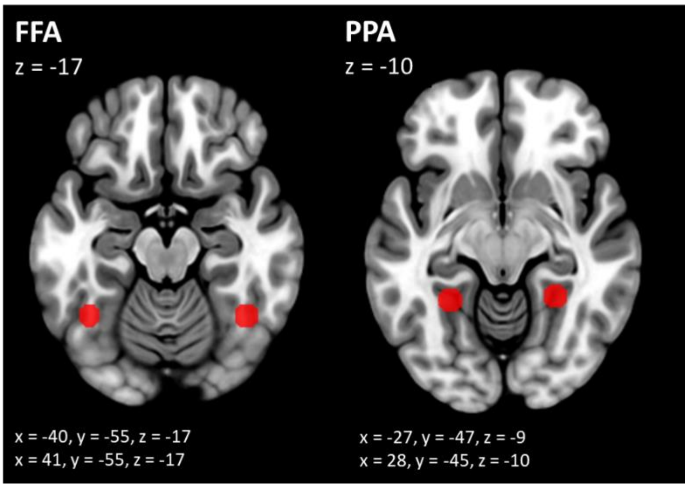

Figure 2. Location of FFA and PPA ROIs obtained from the functional localizer, averaged across participants.

Eye movement data analysis

Eye movements of 24 participants were recorded with a long-range optics infrared eye tracker (EyeTrac 6, Applied Science Laboratories, Bedford, USA). Eye data of six participants were not recorded due to technical difficulties. Data were collected at a sampling rate of 120 Hz. Fixation epochs were computed to determine whether participants refrained from eye movements during trials. A fixation epoch started when six consecutive samples fell within a standard deviation of 0.5 visual degrees. It ended when three consecutive samples fell outside of a 1.5-degree ellipse around the original fixation point. Trials that were completely within one fixation epoch were marked as fixation trials.

The percentage of fixation trials per participant and condition was computed. These percentages were subjected to a 2×2 repeated-measures ANOVA with the factors Task (face vs. house) and Effort (low effort vs. high effort) to check for differences in eye movements between conditions.

Results

Behavior

Target detection task: d’

Effects are displayed in Figure 3A. A main effect of Task was found, with higher d’ scores on the face task ($M = 2.46$) than on the house task ($M = 2.15$), $F(1, 29) = 23.21$, $p < 0.001$. A main effect of Effort was also present, with higher d’ scores in the low-effort condition ($M = 3.72$) than in the high-effort condition ($M = 0.89$). An interaction between Task and Effort was found, $F(1, 29) = 5.06$, $p = 0.032$, indicating that the difference between low- and high-effort conditions was larger on the face task ($M = 3.96$ vs. 0.97) than on the house task ($M = 3.50$ vs. 0.82). Importantly, the d’ scores of all four conditions differed from zero (p’s < 0.001), including the high-effort face condition, $t(29) = 11.72$, $p < 0.001$, and the high-effort house condition, $t(29) = 13.68$, $p < 0.001$. This indicates that participants were engaged in the task and able to discriminate between target-present and target-absent trials, also on the high-effort blocks.

Subjective rating task

The subjective ratings are displayed in Figure 3B-C. A main effect of Effort on difficulty rating was found, with higher ratings in the high-effort ($M = 71.2$) than in the low-effort condition ($M = 23.2$), $F(1, 31) = 157.62$, $p < 0.001$ (Figure 3B). No other effects on difficulty rating were found, p’s > 0.43. A main effect of Effort on effort investment rating was also found, with higher ratings in the high-effort condition ($M = 59.0$) than in the low-effort condition ($M = 28.7$), $F(1, 31) = 58.02$, $p < 0.001$ (Figure 3C). No other effects on effort investment rating reached significance, p’s > 0.37.

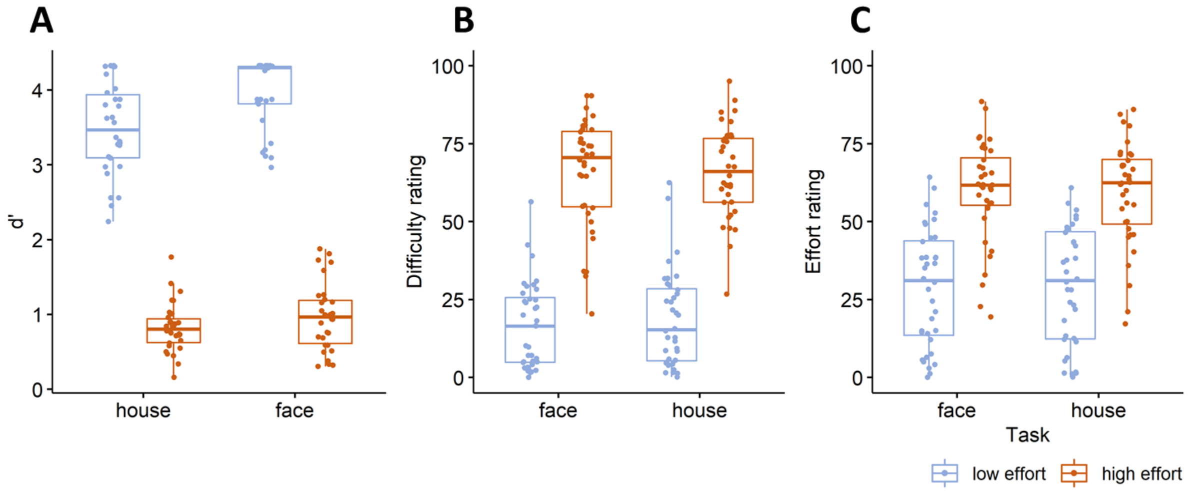

Figure 3. A) d’ scores on the target detection task. *B)* Subjective difficulty ratings. *C)* Subjective effort investment ratings.

fMRI results

Task-specific effects

Table 1 displays task-specific activation patterns in the low- and high-effort conditions. As anticipated, areas related to the processing of faces, such as right FFA and superior temporal sulcus showed increased activation in the low-effort condition of the face task (vs. the low-effort house condition). After small volume correction, increased activity was also found in left FFA for this contrast. On the low-effort house task (vs. the low-effort face task), areas responsive to house images, such as bilateral PPA, showed increased activation. In the high-effort condition of the face task (vs. the high-effort house condition), activation in bilateral FFA was found after small volume correction. In the high-effort house condition (vs. the high-effort face condition), bilateral PPA was activated. This shows that FFA and PPA were involved in the low- *and* high-effort condition, even despite the minor perceptual evidence in the high-effort condition.

Effort-specific effects

To investigate brain areas that are involved in effort investment in a task-general way, we first mapped areas responsive to high-effort demands in both tasks. In the face task, this revealed stronger activation when effort was high (vs. low) in a network constituting dACC (extending into pre-SMA), bilateral AI, bilateral IPS, bilateral middle occipital gyrus (MOG), right IFG, left cerebellum, and right dlPFC (Table 2, Figure 4A). In the house task, we found effort-induced activation in right dACC (extending into pre-SMA), bilateral AI, right IPS, and bilateral MOG (Table 2, Figure 4B). Next, a conjunction analysis was performed on the two contrasts. This revealed that voxels in right dACC, bilateral AI, and right IPS were conjointly activated (Table 2, Figure 4C), showing that activation in these areas scaled with effort, independent of the task at hand.

Finally, no significant activation was found for the interaction between Task and Effort.

Functional connectivity

For the gPPI analysis, the dACC cluster that showed activation in the high- versus low-effort conjunction analysis was used as a seed. When comparing high- to low-effort demand in the face task, increased connectivity was found between dACC and multiple regions, including bilateral FFA (Table 3, Figure 5A). The same contrast on the house task showed activation in several regions including right PPA and right FFA (Figure 5B). An interaction contrast comparing effort effects between the face and house task (i.e., [FaceHE > FaceLE] vs. [HouseHE > HouseLE]) revealed no significant activation.

To further investigate these connectivity patterns, we conducted an ROI-to-ROI gPPI analysis with the same dACC seed and the participant-specific (left and right) PPA and FFA ROIs obtained through the localizer task. This showed increased connectivity between dACC and the set of target ROIs (left PPA, right PPA, left FFA, and right FFA) when effort demands were high (vs. low) in the face task, $F(4, 26) = 6.84$, $p < 0.001$. Specifically, increased connectivity was found from dACC to left FFA, $\beta = 0.17$, $t(29) = 4.54$, $p < 0.001$, and right FFA, $\beta = 0.16$, $t(29) = 4.63$, $p < 0.001$ (Figure 6A). When effort demands were high (vs. low) in the house task, increased connectivity between dACC and the set of target ROIs was also observed, $F(4, 26) = 4.45$, $p = 0.007$. Specifically, this connectivity was from dACC to left PPA, $\beta = 0.11$, $t(29) = 2.78$, $p = 0.015$, right PPA, $\beta = 0.13$, $t(29) = 3.65$, $p = 0.004$, and right FFA, $\beta = 0.11$, $t(29) = 2.70$, $p = 0.015$ (Figure 6B). Crucially, the interaction contrast comparing effort effects between the face and house task (i.e., [FaceHE > FaceLE] vs. [HouseHE > HouseLE]) showed directly that connectivity patterns differentiated between tasks, $F(4, 26) = 7.44$, $p < 0.001$ (Figure 6C). Effort-increased connectivity from dACC to left FFA was larger on the face task, $\beta = 0.16$, $t(29) = 3.65$, $p = 0.004$, while effort-increased connectivity from dACC to left PPA, $\beta =- 0.12$, $t(29) = -2.29$, $p = 0.040$, and right PPA, $\beta = -0.12$, $t(29) = -2.83$, $p = 0.017$, was larger on the house task.

Table 1. *Summary of the task-specific activation clusters.*

		Cluster-level statistics		**Peak-level statistics**			
					MNI coordinates		
Region	**Side**	**Size**	***p*(FWE)**	***t*-value**	**X**	**Y**	**Z**
Low effort: Face > House							
Superior temporal sulcus	R	427	<0.001	5.77	58	-58	10
Fusiform face area	R	128	0.018	5.24	42	-60	-20
Precuneus	R	279	<0.001	4.94	2	-50	42
Fusiform face area*	L	21	0.013	4.69	-42	-62	-18
Low effort: House > Face							
Parahippocampal place area	R	457	<0.001	8.50	24	-42	-10
Parahippocampal place area	L	288	<0.001	6.72	-24	-46	-10
Occipito-temporal cortex	R	495	<0.001	6.21	38	-78	14
Occipito-temporal cortex	L	303	<0.001	5.43	-32	-88	12
High effort: Face > House							
Fusiform face area*	R	74	0.002	5.45	40	-46	-18
Fusiform face area*	L	55	0.003	5.20	-40	-46	-18
High effort: House > Face							
Parahippocampal place area	R	256	0.001	7.09	34	-40	-8
Parahippocampal place area	L	213	<0.001	6.82	-26	-44	-10

* After small volume correction using a sphere with 10-mm radius centered at the peak-voxel coordinates obtained from the localizer (Figure 2).

Table 2. *Summary of the activation clusters on the high- versus low-effort contrasts.*

		Cluster-level statistics		**Peak-level statistics**			
					MNI coordinates		
Region	**Side**	**Size**	***p*(FWE)**	***t*-value**	**X**	**Y**	**Z**
Face task: high effort > low effort							
Anterior insula	R	546	<0.001	8.63	32	20	-4
Dorsal anterior cingulate cortex	R	919	<0.001	8.07	8	24	40
Anterior insula	L	406	<0.001	7.62	-34	20	-2
Intraparietal sulcus (extending into middle occipital gyrus)	R	2084	<0.001	7.56	38	-78	12
Middle occipital gyrus	L	1085	<0.001	6.93	-30	-82	14
Intraparietal sulcus	L	209	0.002	6.12	-28	-50	50
Inferior frontal gyrus	R	361	<0.001	5.89	48	10	22
Cerebellum	L	164	0.006	5.87	-6	-74	-28
Dorsolateral prefrontal cortex	R	108	0.043	5.54	40	36	18
House task: high effort > low effort							
Anterior insula	R	675	<0.001	6.69	38	20	-2
Dorsal anterior cingulate cortex	R	309	0.001	5.77	4	22	44
Anterior insula	L	359	<0.001	5.23	-30	26	-2
Intraparietal sulcus (extending into middle occipital gyrus)	R	392	<0.001	5.01	24	-62	30
Middle occipital gyrus	L	202	0.002	4.56	-30	-88	22
Conjunction (high effort > low effort in face task & house task)							
Anterior insula	R	526	<0.001	6.11	36	20	-4
Anterior insula	L	306	<0.001	5.52	-34	20	-4
Dorsal anterior cingulate cortex	R	276	0.001	5.04	6	24	40
Intraparietal sulcus	R	247	0.002	4.97	24	-62	30

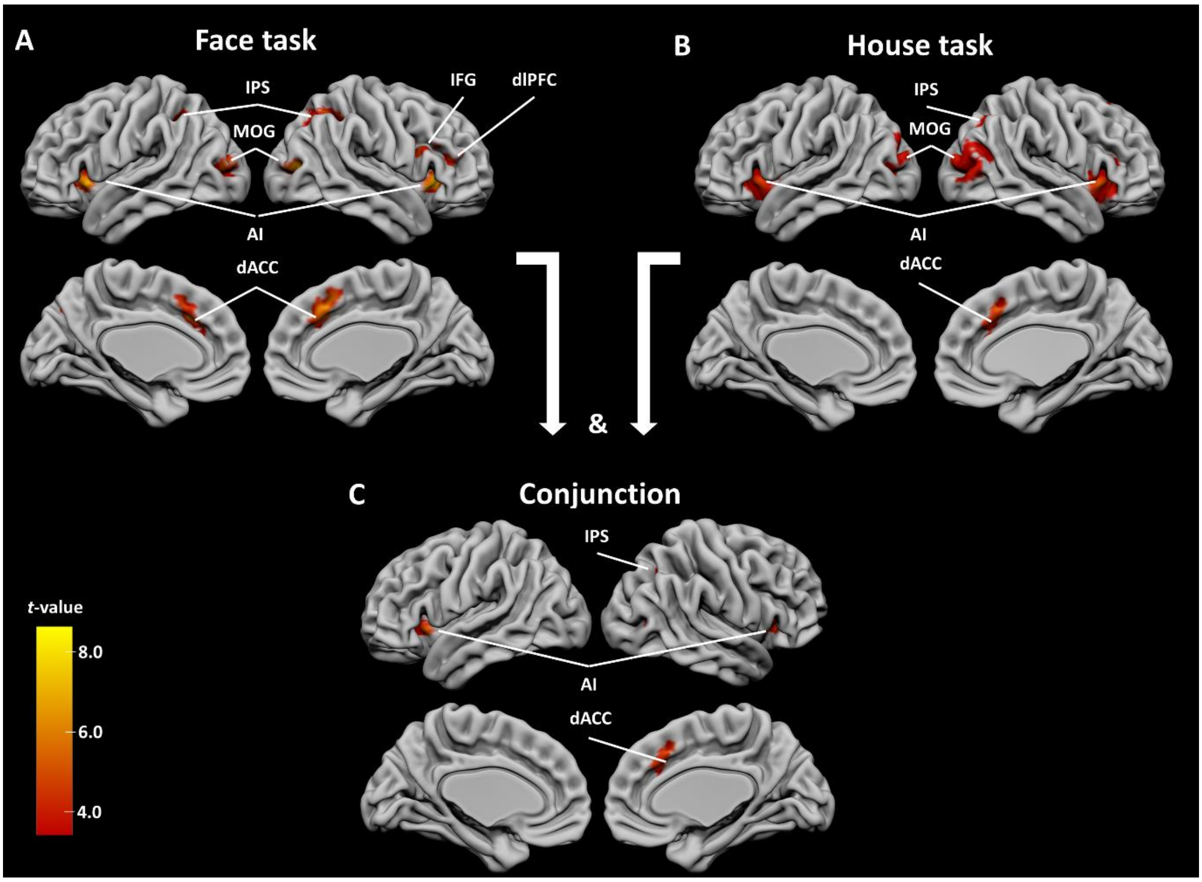

Figure 4. Brain activation in the high- versus low-effort demand condition on *A)* the face task and *B)* the house task. *C)* Conjunction analysis showing mutual activation for the high- vs. low-effort demand condition on both the face and house tasks. AI = anterior insula, dACC = dorsal anterior cingulate cortex, dlPFC = dorsolateral prefrontal cortex, IFG = inferior frontal gyrus, IPS = intraparietal sulcus, MOG = middle occipital gyrus.

Table 3. *Summary of the activation clusters from the gPPI analysis*

		Cluster-level statistics		**Peak-level statistics**			
					MNI coordinates		
Region	**Side**	**Cluster size**	**p(FWE)**	***t*-value**	**X**	**Y**	**Z**
Face task							
Occipital pole	L	670	<0.001	6.67	-12	-94	-12
Fusiform face area	L	89	0.026	5.72	-42	-52	-20
Fusiform face area	R	222	<0.001	5.67	36	-48	-20
Occipital pole	R	111	0.008	4.64	18	-84	12
House task							
Temporo-occipital, including PPA and FFA	R	1425	<0.001	6.36	36	-86	8
Lateral occipital superior	L	881	<0.001	5.97	-28	-78	22
Precentral gyrus	L/R	116	0.006	5.02	0	-8	66
Supplementary motor area	L	191	<0.001	4.92	-32	-12	48
Lateral occipital inferior	L	79	0.045	3.86	-46	-74	-8

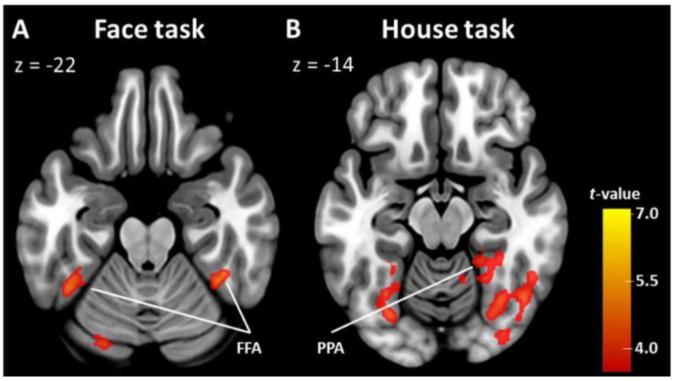

Figure 5. Whole-brain connectivity with dACC. The connectivity values are contrasted between high and low-effort demands in *A)* the face task and *B)* the house task. FFA = fusiform face area, PPA = parahippocampal place area.

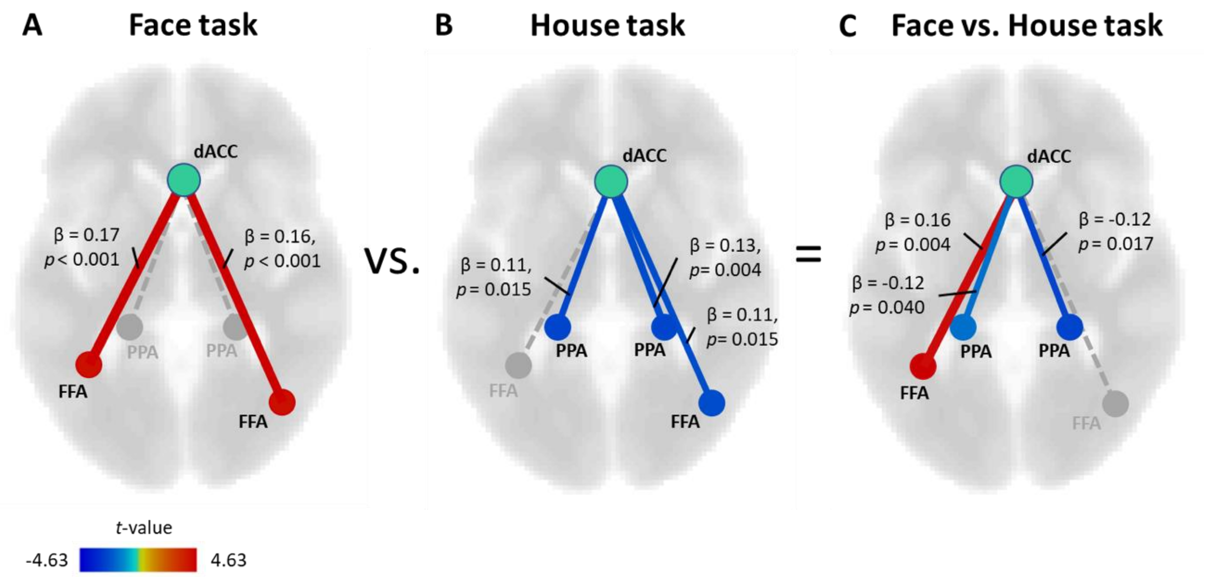

Figure 6. ROI-to-ROI connectivity results with dACC as seed and bilateral FFA and PPA as target regions. Effort-induced connectivity on A) the face task and B) the house task. C) Difference between A and B: difference in effort-increased connectivity between the face and house task. Red = increased connectivity on face task, blue = increased activity on house task. Width of the lines corresponds to strength of effects.

Eye movements

Analysis of the eye movement data revealed no main effect of Task, *F*(1, 23) = 0.05, *p* = 0.83, or Effort, *F*(1, 23) = 2.01, *p* = 0.17, or an interaction between Task and Effort, *F*(1, 23) < 0.01, *p* = 0.98. These findings were confirmed through the computation of Bayes Factors (BF_{01}), which showed evidence in favor of the null hypothesis and not in favor of a Task effect, BF_{01} = 4.71, nor of an Effort effect, BF_{01} = 1.38. There was also more evidence for the null model compared to a model with both Task and Effort, BF_{01} = 6.49, and compared to a full model that included both effects and their interaction, BF_{01} = 32.0. On average, participants fixated on 33.2% of the trials, meaning they generally adhered poorly to the instruction to refrain from eye movements but did so in every condition equally.

Discussion

Effort investment is thought to be implemented in a hierarchical manner with a crucial role for dACC at the top of this hierarchy (Holroyd & Yeung, 2012; Shenhav et al., 2013; Verguts et al., 2015). In this study, we investigated *how* this effort investment is implemented in the brain. We used a face detection task and a house detection task with different effort levels, and showed that increased effort investment is reflected in a general increased activation of dACC and related areas, independent of the task at hand. Importantly, we also showed an effort-induced strengthening of connectivity between dACC and specialized lower-level perceptual areas, depending on the performed task. The increased functional connectivity between dACC and lower-level areas emerged in the high-effort condition, where effort investment was rated higher. Note that this increased connectivity occurred while activation in FFA and PPA did not differ between both effort conditions. This connectivity was also task-specific: Stronger dACC-FFA connectivity was found when high- versus low-effort faces had to be detected, while stronger dACC-PPA connectivity was found when high- versus low-effort houses had to be detected. This fits with the proposed hierarchical position of dACC, allocating resources to task-relevant areas.

One interpretation of the connectivity findings is that dACC amplifies the signal in task-relevant areas, in order to increase performance in difficult conditions. In the present study, the signal-to-noise ratio of images in the high-effort conditions was low, meaning that they lacked strength to elicit robust bottom-up activation of FFA or PPA. Such activation is needed to make accurate decisions on the content of the presented image (Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Lamichhane & Dhamala, 2015; Tremel & Wheeler, 2015). The increased connectivity between dACC and perceptual areas may serve as a compensatory mechanism for the lack of clear perceptual evidence present in the stimulus. Since participants knew beforehand what type of stimulus they had to detect, increased input from dACC may function to optimize neural processing of the stimulus by specialized areas (FFA or PPA).

The exact neural mechanism underlying this optimization may be explained by response-sensitization of task-relevant areas. There are several ways how this might be implemented. For example, it has been proposed that stimulus-induced dynamics in cortical areas can be augmented by increasing their background activity (Beck & Kastner, 2009; Chawla, Rees, & Friston, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). This may result in an increased synchronization of the neurons representing a stimulus (Buschman & Kastner, 2015; Fries, Reynolds, Rorie, & Desimone, 2001). In addition, top-down influences may also decrease noise correlations between neurons in a region. Decreased noise correlations lead to an increase of the signal-to-noise ratio and hence the amount of information encoded by the neuronal ensemble (Gilbert & Li, 2013; Ramalingam, McManus, Li, & Gilbert, 2013). Yet another explanation may be a top-down induced increase in neural gain in task-relevant regions (Aston-Jones & Cohen, 2005). Increasing gain suppresses weak activation (typically, noise) and increases strong activation (typically, signal), thus functionally increasing signal-to-noise ratio. Processes like these can give a cortical area an advantage in subsequent stimulus processing (Egner & Hirsch, 2005).

On a neural level, cognitive effort investment can thus be seen as an attempt to overcome a compromised signal in a population of neurons. This idea can also be applied to neuronal fatigue, where adaptation may lead to reduced signal-to-noise ratio in a brain area, as a result of repeatedly performing a cognitive action. To compensate for this neuronal fatigue, effort may be implemented as a stronger control signal that establishes the necessary signal-to-noise ratio in in the relevant neural population (Müller & Apps, 2019).

We also found that activity in dACC scaled with the level of effort investment, independent of the task. In the high-effort conditions, larger dACC activity was found than in the low-effort conditions. Conjunction analysis showed that this was true for both the face- and house-detection task, with jointly activated dACC, bilateral AI, and right IPS. These areas thus constitute a task-independent network of brain regions involved in effortful behavior. Within this network, the importance of dACC for effortful behavior converges with model simulations showing that dACC-lesioned rats are less likely to engage in effortful behavior (Holroyd & Mcclure, 2015), and by the fact that dACC lesions are associated with a lack of motivation or anergia (Cohen et al., 1999; Holroyd & Yeung, 2012; Walton, Bannerman, & Rushworth, 2002). It is also consistent with studies relating dACC activity to self-reported effort investment (Mulert, Menzinger, Leicht, Pogarell, & Hegerl, 2005), will to persevere (Parvizi, Rangarajan, Shirer, Desai, & Greicius, 2013), and anticipation of effortful tasks (Chong et al., 2017; Croxson, Walton, Reilly, Behrens, & Rushworth, 2009; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Prevost, Pessiglione, Metereau, Clery-Melin, & Dreher, 2010). One difference with the latter studies is that they appoint to dACC a role in integrating effort costs and reward values and deciding whether or not it is worthwhile to invest a given level of effort. In the present study, no reward was offered and no cost-benefit decision had to made, indicating that dACC also operates whenever more effort is required, regardless of cost-benefit decisions (see also Engström et al., 2015; Vassena et al., 2014).

Alternative descriptions of the function of dACC exist as well. For example, the smaller perceptual difference between target-present and target-absent trials in the high-effort condition may have triggered response conflict. This conflict may have served as the indicator to allocate additional cognitive effort, reflected in conflict-induced activation of dACC in the high-effort condition (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, 2012; Shenhav et al., 2013). Relatedly, dACC activity in the high-effort conditions may also reflect the role of the region in maintaining effortful control over task performance, protecting the actor against conflict (Holroyd & Yeung, 2012).

Further, dACC activity has also been linked to pain (Rainville, Duncan, Price, Carrier, & Bushnell, 1997), and error monitoring (Bush, Luu, & Posner, 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993). However, these factors are unlikely to play a role in the current paradigm. No pain was involved and there is also not much opportunity for error monitoring for two reasons. First, participants did not receive trial feedback. Second, it is hard to become metacognitively aware of an error in the high-effort condition because there is never clear evidence in favor of one of the two response options. In addition, participants had to withhold their responses for one second. This is different from speeded response tasks where participants occasionally slip and make an error while the correct response is readily available. In such cases, participants often do become aware of the error they made, even without feedback.

Together with dACC activity, we also observed effort-induced activity in bilateral AI and right IPS on both tasks. These regions are often conjointly activated, together with dlPFC, on a wide range of cognitive tasks that demand attention, working memory, or cognitive control (Corbetta & Shulman, 2002; Dosenbach et al., 2006; Menon & Uddin, 2010; Nelson et al., 2010; Shenhav et al., 2017). The coactivation of dACC and AI is particularly common, which might be due to their strong structural connectivity (Allman et al., 2010; Cauda et al., 2013). AI has traditionally been related to detection of salient events (Downar, Crawley, Mikulis, & Davis, 2002; Menon & Uddin, 2010) and attentional control (Nelson et al., 2010). In the present study, saliency of the presented stimuli was constant. The function of AI therefore seems more consistent with accounts postulating that AI subserves maintenance of a task-set (Dosenbach et al., 2006; Menon & Uddin, 2010), or tonic alertness (Sadaghiani & D'Esposito, 2015). Such processes may have been more profound in the high-effort conditions. For example, a (tonic) activation of AI in high-effort conditions may alert the system that the demand to detect a target is higher (Han, Eaton, & Marois, 2019). This way, dACC may also be informed to intensify its control signal to task-relevant areas.

In conclusion, we showed increased effort-induced connectivity between dACC and lower-level perceptual areas (FFA or PPA), specific to the performed task. Dorsal ACC was part of a broader network consisting also of AI and IPS, that is more strongly activated when effort demands are high, independent of the task at hand. We conclude that dACC, AI, and IPS constitute a general effort-responsive network and that the neural implementation of cognitive effort involves dACC-initiated response-sensitization of task-dependent areas.

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5

General discussion

As actors in an increasingly complex world, our cognitive systems are taxed by an almost endless flow of information. To handle this bulk of information efficiently, and maintain a comprehensible mental representation of our surroundings, we must exert effortful cognitive control. We need cognitive control to prioritize relevant over irrelevant information, attend to important details and resist distractions, or inhibit automatic responses in favor of more appropriate actions. Throughout this dissertation, cognitive control was treated as the force through which cognitive effort is implemented, and cognitive effort as the intensity at which cognitive control is exerted. It was also argued that in line with neuroeconomic approaches, effortful control is costly (Botvinick & Braver, 2015; Kool & Botvinick, 2018; Shenhav et al., 2017). People will try to avoid effort and only invest it if the expected gain (i.e., reward) exceeds the expected cost of applying control (Shenhav, Botvinick, & Cohen, 2013). For this reason, effortful control may be implemented with different temporal profiles (Braver, 2012), each with specific effort demands and different behavioral and neural signatures.

Indeed, part of this dissertation was built on the idea that temporal variations in control exist. Control modes roughly range from transient to sustained control, and are affected by the frequency of experienced conflict. When conflict is rare, transient control is optimal because it is only applied occasionally and therefore spares effort. When conflict is frequent, this strategy is inefficient and replaced by sustained control. The prolonged nature of this control mode makes it effortful. These temporal variations in control mode take a prominent position in several dual-mode frameworks on effortful control (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, 2012; Jiang, Heller, & Egner, 2014; Ridderinkhof, 2002), which motivated the development of a behavioral quantification of the time scale of control. This was the objective of the study in chapter 2.

An important prediction that can be derived from dual-mode frameworks of effortful control is that if control indeed can be applied in a sustained way, this should be reflected in increased neural activity in the interval between trials, when conflict is frequent. Although there is some debate on whether this should occur in the same brain regions that are involved in transient control (Braver, 2012) or not (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Gratton, Sun, & Petersen, 2018), there is consensus that a truly sustained control mode is anticipatory, which means it should be mirrored in increased brain activation not only during trial performance but also before a trial is encountered. This principle was assessed in chapter 3.

Whereas chapters 2 and 3 were concerned with the issue *when* cognitive effort is applied, there is also the question *how* effort investment is implemented exactly (or: through what neural mechanism). Several theories suggest that dorsal anterior cingulate cortex (dACC), as part of a broader network of brain regions, tracks the effort demand of a task, and may exert its effect on task-specific processing by energizing upstream areas (Holroyd & Yeung, 2012; Shenhav et al., 2013; Verguts, Vassena, & Silvetti, 2015). These principles were assessed in chapter 4, where effort-induced activation and connectivity of dACC were compared across slightly different tasks.

Together, the three empirical studies in this dissertation assessed the temporal and task-specific investment of cognitive effort. In this general discussion, the main findings of the studies will first be summarized and integrated. This is followed by a critical evaluation of the utility of current empirical measures for cognitive control, and a discussion of the role of dACC and lateral prefrontal cortex (lPFC) in effort investment. Next, the potential reasons why effortful control is costly are explored, followed by a consideration of the relation between cognitive and physical effort. Finally, avenues for future research are proposed and a conclusion is provided.

Research findings

In **chapter 2**, a behavioral index of the time scale of control was developed. The chapter examines *when* effortful control is applied. Inspired by reinforcement learning, the index extends the widely investigated congruency sequence effect (CSE) from one trial to multiple trials into the past. It assesses the degree to which current effort implementation is affected by recency of experienced conflict. When current behavior is mainly affected by conflict encountered on the preceding trial and less by more remote trials, cognitive control adjustments are quick. This means that cognitive control operates on a short time scale. This transient control mode spares effort because control is only exerted just in time, when needed. When current behavior is also affected by conflict that was experienced on more remote trials, cognitive control adjustments are slow. In this case, cognitive control operates on a longer time scale. This sustained control mode is more effortful but has the important advantage that task performance will be better in contexts where conflict is frequent.

The results of chapter 2 confirm that control is applied on a longer time scale when conflict is frequent versus when conflict is rare. This corroborates the existence of time scale variations in cognitive control (Botvinick et al., 2001; Braver, 2012; Jiang et al., 2014; Ridderinkhof, 2002), that may serve to efficiently balance task performance and costly cognitive effort. The chapter also shows that in volatile contexts where control demand fluctuates, control is characterized by fast adaptations. This short time scale of control is consistent with the instability of the context, which requires continuous adjustments to changing demands. Importantly, the empirical measure developed in chapter 2 allows for a fine-grained assessment of the temporal dynamics of effort investment, capable to capture (subtle) differences in control mode in a dynamic way. The time-scale measure also closely corresponds to the amount of effort invested in a task, with short time scales being less effortful than long time scales.

The differentiation of control into distinct temporal modes is for a large part based on the assumed underlying temporal variation in neural activity patterns (Botvinick et al., 2001; Braver, 2012; Carter et al., 2000; De Pisapia & Braver, 2006). It is suggested that transient control is resembled by short-lived activation of control-relevant brain areas. This activation occurs right at the moment when control is needed. Sustained control should be reflected in prolonged neural activation across a longer stretch of time, even during intervals where control is not needed. In **chapter 3**, we directly tested whether transient and sustained control indeed have these corresponding neural profiles. In this fMRI study, we compared on-trial and inter-trial activity in MC versus MI contexts. Control exerted on a short time scale was mirrored in brief fronto-parietal activation on incongruent (vs. congruent) trials that was stronger when these trials were embedded in an MC compared to an MI context. This pattern of activity is to be expected if one assumes that conflict has an intrusive effect in situations where the actor is off guard. This is the case in the MC context, where control is only required occasionally and the actor mainly relies on effortless automatic behavior. A sudden encounter of an incongruent trial then mobilizes cognitive control at the last moment. In the MI context, on the other hand, the actor is on guard all the time, meaning that the control signal is high on all (i.e., incongruent *and* congruent) trials. This effortful strategy protects the actor against the intrusive effects of repeatedly encountered conflict, and may be reflected in a smaller difference in neural response between incongruent and congruent trials in the MI context.

Although suggestive, on-trial activity patterns cannot directly attest to temporal differences in activity profiles of transient and sustained control. The main finding of chapter 3 therefore concerns the context-dependent differences in inter-trial activity, which provide more conclusive evidence. In chapter 3, we demonstrated that brain regions that showed increased transient (i.e., on-trial) activity in the MC context (i.e., intraparietal sulcus, IPS; dorsolateral prefrontal cortex, dlPFC; and midfrontal gyrus, MFG) also showed increased sustained (i.e., between-trial) activity in the MI context. This is a more direct demonstration of the sustained nature of control in contexts that demand frequent cognitive control. Assuming that sustaining neural activation is costly (see below), these findings are consistent with the results of chapter 2, showing that cognitive control is implemented flexibly in order to balance task performance against effort cost.

In **chapter 4**, the focus is on *how* effort investment is achieved in the human brain. It is generally assumed that dACC is a crucial hub that allocates effort based on the goals of the actor. Depending on these goals and the task, specialized brain areas may be recruited. This prediction was tested in an fMRI study where participants performed a task that required them to either detect a face or a house. Participants had to do so in conditions that required either low or high cognitive effort. An effort-induced network of brain areas consisting of dACC, anterior insula (AI), and IPS was found to be activated independent of the performed tasks. More crucially, functional connectivity profiles differed between the two tasks. Effort-induced connectivity was stronger between dACC and fusiform face area (FFA) when subjects had to detect a face, and stronger between dACC and parahippocampal place area (PPA) when subjects had to detect a house. This demonstrates how dACC connects more strongly to task-relevant areas when effort is high, possibly resulting in response-sensitization of these regions.

Taken together, **chapters 2, 3, and 4** expose the temporal and task-specific profiles of effortful control. The results can be united under neuroeconomic theory: effortful control is costly and people seek strategies to minimize effort expenses while maintaining an acceptable level of performance. On this view, transient control is generally preferred over sustained control because it is effort sparing. Transient and sustained control are therefore implemented flexibly: when transient control results in suboptimal performance, as is for example the case when cognitive conflict is frequent, sustained control will be applied. Sustained control benefits performance because the actor will be less distracted and conflict will have less opportunity to impair behavioral responses. However, it also increases effort expenditure, for example because it requires maintenance of task goals. In terms of neural processing, sustained control is mirrored in maintained activity in the same control-relevant brain areas that are reactivated when transient control is applied.

The reason why cognitive control is costly and preferably avoided remains unknown. Sustained control may be neurally expensive because retaining task-relevant information in active firing mode is metabolically costly or occupies neural pathways that cannot be used for other tasks (see “Why is cognitive control costly” below). Either way, the costly nature of control signals the need for an efficient neural system for effort allocation. dACC seems to be crucial here, as it tracks effort demands and appears to energize task-specific areas when the task is difficult and the effort demand is high. In order to counter performance deterioration on difficult tasks, increased effort may be implemented through increased connectivity between dACC and lower-level areas. This may lead to amplification or denoising of the signal in task-specific areas. Effort may thus compensate for the compromised quality of the bottom-up input offered by the task (e.g., a noisy face in a picture, or a degraded word). This controlled process is not required when the information is of such a quality that it can be processed automatically (e.g., when a face is clearly detectable in a picture, or a word is clearly readable).

Measuring temporal variations in effortful control

Throughout this dissertation, transient (effort-sparing) control was contrasted to sustained (effortful) control. This differentiation is most prominently represented in the dual mechanisms of control framework that contrasts reactive to proactive control (Braver, 2012). Depicting a cognitive construct in dual processes is appealing from a theoretical perspective. Dual systems are easy to grasp;

ironically, the effort that is needed to deal with a reality that might be more complex or nuanced can be avoided. Dualization is therefore an efficient way of categorizing and allows for straightforward experimental designs and statistical analyses. The consequence is that dual models of cognition are almost inevitably a simplification of reality. This is not necessarily a bad thing and probably a prerequisite to progress research on a complex topic such as human cognition. If a model becomes too complex, its scope may become limited to specific instances and the explanatory power of the model may be reduced. Therefore, simple models are often preferred because, although they may be biased, they can be applied more generically. However, too much simplification may also lead to models that no longer capture reality accurately, or are insensitive to subtle differences in the behavior they aim to explain.

In chapter 2, we initially also categorized cognitive control into transient and sustained modes, through assessment of the congruency effect (CE) in MC and MI contexts, respectively. The CEs were used to compute the proportion congruency effect (PCE), which can be used to infer the context-dependent application of transient and sustained control. However, we subsequently also indexed cognitive control modes on a continuous time scale on which control ranged from rapid to slow adjustments. Although the results were consistent with theories proposing that cognitive control can be applied in a transient or sustained way (Botvinick et al., 2001; Braver, 2012; Jiang et al., 2014; Ridderinkhof, 2002), the quantitative measure we computed is likely to be more sensitive to capture trade-offs between control modes than classical measures such as the CSE or PCE. For example, evaluating control on a continuous dimension has the advantage that there is no need to create dichotic conditions such as MC and MI contexts to elicit transient and sustained control. In chapters 2 and 3, such manipulations were performed. The starting point of these chapters was that MC and MI contexts trigger transient and sustained control modes. It is known that approaching reality in a dichotic way can have detrimental effects on research outcomes. By simplifying complex data into two categories (e.g., MC = transient/reactive control vs. MI = sustained/proactive control) information is lost, statistical power and effect sizes decrease, and complex (non-linear) relationships may be overlooked (MacCallum, Zhang, Preacher, & Rucker, 2002). For these reasons, it is desirable to have a more refined way to measure differences in cognitive mechanisms, which is offered by evaluating control modes on a single continuous scale, as we did in chapter 2. The results of this chapter also imply that the idea that transient (reactive) and sustained (proactive) control reflect two distinct, independent mechanisms (most explicitly expressed in Gonthier, Braver, & Bugg, 2016; see also Braver, 2012; Braver, Gray, & Burgess, 2007), should be nuanced. They suggest that these mechanisms are better perceived as the poles of a single dimension.

By indexing control on a single scale, different groups or conditions can also be compared without the need to set the stage a priori (e.g., creating conditions that elicit transient and sustained control, such as MC and MI contexts). For example, one simple Stroop task with 50% incongruent trials can be used to investigate if the default control mode of schizophrenic patients differs from that of healthy controls. Compared to matched controls, schizophrenic patients may adjust their control settings only based on recent experiences of conflict but not based on more remote experiences, which would indicate a shorter time scale of control. Likewise, to assess the effects of cognitive load on control mode, participants could be asked to perform a 50% incongruent Stroop task under low and high working memory demand. In these examples, the temporal mode of control can be measured with the method of chapter 2, which obviates the need to first map sustained and transient control on specific tasks or contexts and allows for simplification of the experimental design.

The role of dACC and lPFC in effort investment

In chapter 4, dACC activation was found to scale with effort investment, which is in accordance with many cognitive theories and experimental findings. This activation extended into pre-SMA. In chapter 3, however, no control-related activity was found in dACC. Although these studies involve heterogenous control signals, dACC activity was expected in both studies, given that dACC has been extensively linked to cognitive control and/or cognitive effort (Botvinick et al., 2001; Braver, 2012; Cole & Schneider, 2007; De Pisapia & Braver, 2006; Holroyd & Yeung, 2012; Shenhav et al., 2013; Wilk, Ezekiel, & Morton, 2012).

It remains speculative what the exact reason is for the absence of dACC activity in chapter 3. It might be due to specifics of the task, as absence of dACC activity is not uncommon when flanker tasks are used (Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Nee, Wager, & Jonides, 2007). Also, there exists an association between pre-SMA and cognitive control (Isoda & Hikosaka, 2007; Jahn, Nee, Alexander, & Brown, 2016). In chapter 3, control-related activity was observed in pre-SMA, which is consistent with previous work. For example, Horga and colleagues (2011) showed that pre-SMA, and not so much dACC, responded to conflict and that this response closely mirrored behavioral performance. It is also clear that dACC and pre-SMA are closely related and sometimes hard to separate, both anatomically and functionally. They are both part of the medial frontal cortex, an area that is known for its heterogenous responses (De La Vega, Chang, Banich, Wager, & Yarkoni, 2016). Although attempts have been made (Jahn et al., 2016; Nee, Kastner, & Brown, 2011), it remains unclear what the exact commonalities and differences are between dACC and pre-SMA. It is also important to note that the connectivity analyses in the Supplemental Material of chapter 3 showed increased connectivity between IPS and dACC when effortful sustained control was applied. This bears resemblance to the connectivity results of chapter 4, where dACC showed stronger connections with task-relevant areas in high-effort conditions.

Another aspect that deserves attention is the finding that dlPFC was activated in chapter 3, but not (consistently) in chapter 4. It is often claimed that dlPFC, as a part of lateral PFC (lPFC), plays a key role in the implementation of cognitive control through its close collaboration with dACC (Botvinick et al., 2001; Braver, 2012; Corbetta & Shulman, 2002; Dosenbach et al., 2008; Kerns, 2006; MacDonald, Cohen, Stenger, & Carter, 2000; Menon & Uddin, 2010; Power et al., 2011; Smith et al., 2019). That is, dACC is thought to monitor the effort and the type of control required to solve a task, outputs this result to lPFC, which in turn regulates the implementation of the control signal to a given task. However, the consistency of the dACC-lPFC collaboration has been questioned by studies that showed an absence of dACC-lPFC associations in the implementation of control (Hyafil, Summerfield, & Koechlin, 2009; Kouneiher, Charron, & Koechlin, 2009; see also below). Yet, it remains unclear what determines the presence or absence of lPFC activity during the application of cognitive control. The results of chapters 2 and 3 underline that implementation of cognitive control is a heterogenous process, whereby brain areas that are supposed to operate task-independently can however be differently activated between tasks.

With regard to chapter 3, the observed on- and between-trial activation of lPFC activity can be explained by the reactivation (in MC contexts) and maintenance (in MI contexts) of the task goal, that may instigate parietally controlled attentional adjustments. This explanation is in accordance with the dual mechanisms of control theory (Braver, 2012), but not consistent with another dual-processes theory that suggests that dACC and AI support stable task-set maintenance, and lPFC instigates rapid adjustments (Dosenbach et al., 2008). According to this latter framework, lPFC should not have shown sustained activity. However, it should be realized that the between-trial analyses in chapter 3 were conducted on ROIs selected based on the on-trial results. In other words, other regions that might play a role in sustained but not transient control may have been missed (e.g., dACC, AI), since they would not have been selected based on on-trial activation.

In chapter 4, effort-induced lPFC activation was only found in the face task. It could be argued that lPFC, as a generic executer of control, should have mediated the functional relation between dACC and task-relevant areas on both tasks (cf. chapter 3). Absence of lPFC activity in the house task could be ascribed to insufficient statistical power. However, Danielmeier and colleagues (2011) showed that lPFC not necessarily has to be involved in control adjustments. They demonstrated that activity enhancement in task-relevant perceptual areas correlated with error-related dACC activity on the previous trial. No correlations between dACC and lPFC were found, nor between task-specific areas and lPFC. This suggests that the effort to reinstall performance after an error is underpinned by functional interactions of the dACC with task-specific areas, without intervention by lPFC. Support for the regulative function of dACC also comes from the involvement of dACC in top-down attentional modulation of auditory versus visual cortical areas (Crottaz-Herbette & Menon, 2006). The results of chapter 3 are inconclusive with regard to the necessity of lPFC in control regulation but may suggest that dACC can also fulfill a regulative function.

The lack of robust lPFC activity in chapter 4 may also be explained by a design characteristic. In study 3, the task goal differed between blocks (i.e. “detect face” or “detect house”) but was similar on every trial within a block. Compared to chapter 3, this may have alleviated working memory demands. In chapter 3, (re)activating task-goals was important on incongruent trials, but not on congruent trials. Incongruent trials may have cued the reactivation of the task goal in the MC blocks, while task-goals may have been kept in a more stable active mode in the MI blocks. These differences between the studies may explain why lPFC activation was found in chapter 3, as the control processes in this study may have taxed working memory more heavily than the processes in chapter 4. It is yet unclear though why working memory demands would be higher in the face task than in the house task of chapter 4, particularly given the better behavioral performance on the first.

Why is cognitive control costly?

As explained before, cognitive control -in its broadest sense- is often contrasted to automatic processing. One of the major aspects that differentiates between controlled and automatic processing is that we can perform multiple automatized tasks at the same time, while we cannot execute multiple cognitive control tasks concurrently. For example, we can watch a movie and simultaneously read the subtitles, but we cannot compute a 20% discount on a sales item and discuss the latest political developments at the same time. Hence, the cost of performing a cognitive control task can be redefined as the cost of not being able to perform another control task concurrently (Cohen, 2018). This limitation of cognitive control is striking since there are no neurophysiological constraints that prohibit the performance of multiple cognitive control tasks at the same time, as will be outlined below. It raises the question why control is perceived as effortful, and hence costly.

A formal definition of the cost of cognitive control was put forward by Kurzban and colleagues (Kurzban, Duckworth, Kable, & Myers, 2013), who applied the concept of opportunity cost to cognitive effort. Briefly, an individual engaged in a cognitive task (e.g., performing mental calculations) will monitor the benefits and costs relative to other operations to which the same cognitive processes might be applied (e.g., playing a game on a smartphone). The more attractive the alternative operation, the higher the opportunity cost. On this view, the experienced opportunity cost of continuing the task, or the value of the next-best possible action, is experienced as effort. Thus, the opportunity cost explains why cognitive tasks are perceived as effortful: because performing one task prohibits us from performing another task. However, it does not explain why this “one task at a time” constraint exists.

One of the first explanations put forward for this constraint was based on resource depletion. It was claimed that cognitive effort investment consumed glucose, just like a muscle consumes energy (Gailliot & Baumeister, 2007; Gailliot et al., 2007). On this view, sustained control would be more effortful than transient control because it is applied on a longer time scale and hence consumes more glucose. This metabolic constraint on cognitive effort has become controversial though, for multiple reasons (reviewed in Kurzban, 2010; Kurzban et al., 2013). First, in an extensive replication study, no or very little evidence for resource depletion theory was found (Hagger et al., 2016). Second, an important argument against the idea of resource depletion is simply that any change in blood glucose level is unlikely to be the result of an increased uptake by the brain (Gibson, 2007). It is more likely the result of increased activity of peripheral organs (e.g., the heart). The changes in blood glucose levels due to cognitive activity are minuscule relative to the brain’s baseline consumption (Kurzban et al., 2013). In fact, within the brain, the largest change in glucose consumption occurs in visual cortex when one simply opens the eyes (Newberg et al., 2005). Yet, visual processes are not perceived as effortful at all, nor sensitive to performance decrements. These findings clearly undermine resource depletion theory.

Another popular explanation for the cost of cognitive effort is framed in structural constraints. The idea is that control relies on one centralized mechanism. This mechanism depends on working memory, which is known to have a limited capacity (Baddeley & Hitch, 1974; Cowan, Rouder, Blume, & Scott Saults, 2012; Kane, Conway, Hambrick, & Engle, 2007; Kane, Bleckley, Conway, & Engle, 2001; Kane & Engle, 2002). Because control (sub)processes typically involve the maintenance and manipulation of information or task goals, they tax the centralized mechanism. Combining one control task with another would then be impossible, because the central mechanism is already fully occupied by the first task. This idea of a structural constraint on cognitive control also resonates in dual-theories of control, that propose that sustained control is more effortful because it requires stronger or prolonged working memory activity (e.g., Braver, 2012). This implies that sustained control occupies the centralized mechanism constantly and no other tasks can be performed for the time being. In transient control mode, automatic and controlled processes alternate, which leaves room for other cognitive activities in the periods where controlled processing is not required. One intuitive objection to a single central mechanism for control is that it seems odd that a system so important for adaptive behavior would be limited to execute one control task at a time. Particularly since these processes rely on the prefrontal cortex, which makes up roughly 30% of the human cortex (Carlén, 2017). It begs the question why evolution and development have not arrived at a more flexible solution that exploits the vast potential of this structure in a more optimal way (Shenhav et al., 2017).

An alternative theory for the costly nature of control is offered by the multiple resource hypothesis (Navon & Gopher, 1979; Shenhav et al., 2017). When multiple tasks involve the same cognitive representations, cross-talk arises, which impairs processing. For this reason, control is restricted to one task at a time. Hence, this restriction reflects the purpose of control rather than an intrinsic limitation of the control system itself, namely to prevent bottlenecks in information processing that occur when tasks make use of overlapping representations. Consistent with this hypothesis, recent work has shown that even modest overlap among neural processing pathways directly limits the number of processes that can be executed at the same time (Feng, Schwemmer, Gershman, & Cohen, 2014; Musslick et al., 2016). In other words, as long as neural networks do not share pathways, multiple processes can be executed simultaneously. When processes depend on networks with overlapping pathways, cross-talk arises. In that case, the number of tasks that can be executed at the same time is limited to one, in order to prevent deterioration in performance (Cohen, 2018). Again, this implicates that sustained control cannot be combined with other cognitive activities that share controlled processing, because it would induce a bottleneck in information processing. Transient control does allow for other controlled processes to be executed, but only in the intervals where no control is needed.

Importantly, the constraint on the use of processes that share representations serves a purpose. Shared representations are critical for abstract learning because they support quick learning and generalization (Rumelhart, Hinton, & Mcclelland, 1986). When a new, non-automatized task must be performed, the brain may benefit from the representations that the new task shares with tasks that were already learned. These shared representations allow efficient learning, and rapid and flexible processing, at the expense of concurrent task execution. This mechanism explains that cognitive control is effortful because it reflects the cost of the single-processing limitation that serves to prevent performance-impairing cross-talk (Shenhav et al., 2017). It also implies that in order for a task to become automatic, an effortful learning process must take place, whereby the representations the task relies on become parallelized. Once these representations have become separated from the representations it overlapped with, the task has become automatized and can be performed effortlessly (Cohen, 2018).

However, parallelizing representations has two costs itself. First, it is a slow process that takes substantial time. For example, it may require 30 hours of driving lessons before the process of driving has become automatized to the degree that the driver can control the car and at the same time read road signs, adhere to the GPS, monitor other traffic, or make conversation with a passenger. Other, more complex tasks, may require even far more time to become automatized, perhaps even beyond a human's lifespan. Second, systems with parallelized representations demand more computational resources, which conflicts with the brain's limited capacity (Cohen, 2018). Independent neural pathways each require dedicated neural structures (i.e., pathways). In analogy, a system with shared representations can be compared to a Swiss knife. Both are efficient "tools" that can be used for many purposes without occupying much space. A Swiss knife takes less space than a separate pocket knife, corkscrew, scissors, bottle opener, and so forth. However, the downside of the Swiss knife is that the corkscrew and the scissors cannot be used at the same time, just like a system of shared representations cannot be used to execute multiple control tasks concurrently.

The consequence of the brain's limited capability for parallel processing is that people often need to rely on heuristics to achieve a goal. This is formalized in resource-rationality, or the idea that the human mind makes rational use of its limited cognitive resources (Lieder & Griffiths, in press). Resource-rationality adopts the concept of bounded rationality, which means that people's performance is limited by cognitive constraints. This is the reason why humans not always operate as rational decision makers but instead rely on bias-prone, but resource-sparse, heuristics. The heuristics are approximations of reality that afford computational simplifications, while maintaining acceptable performance. To achieve resource-rationality, cognitive control must be allocated in such a way that the expected outcome outweighs the time and cognitive resources needed to achieve it (Lieder & Griffiths, in press; Shenhav et al., 2013, 2017). Hence, in addition to protecting the cognitive system against cross talk, cognitive control also optimizes performance given the brain's limited capability for parallel processing (i.e., it achieves bounded optimality).

Cognitive versus physical effort

One lacuna in current literature on effort investment is the poor integration of cognitive and physical effort. The analogy between brain and muscle has been popular but controversial for many years. Although it is appealing to think of the brain as a muscle that can be trained, there is ample debate on the efficacy of such training (e.g., Greenwood & Parasuraman, 2015; Owen et al., 2010), and whether it truly leads to robust neurophysiological changes (Park & Bischof, 2013). Likewise, as argued before, the idea that the brain depletes resources such as blood glucose, just like a muscle depletes energy, is controversial (Hagger et al., 2016; Kurzban et al., 2013). Nevertheless, it is plausible that cognitive and physical effort investment have features in common. Both can lead to feelings of fatigue (Boksem & Tops, 2008; de Morree & Marcora, 2015; Inzlicht & Marcora, 2016; Müller & Apps, 2019), and the costs of cognitive as well as physical effort are tracked by dACC (Botvinick, Huffstetler, & McGuire, 2009; Croxson, Walton, Reilly, Behrens, & Rushworth, 2009; Klein-Flugge, Kennerley, Friston, & Bestmann, 2016; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Massar, Libedinsky, Weiyan, Huettel, & Chee, 2015; Prevost, Pessiglione, Metereau, Clery-Melin, & Dreher, 2010; Schouppe, Demanet, Boehler, Ridderinkhof, & Notebaert, 2014; Westbrook, Lamichhane, & Braver, 2019)

Given this overlap, it is surprising to see that both types of effort are poorly integrated in cognitive theorizing. Some attempts have been made (Müller & Apps, 2019; Shenhav et al., 2013; Verguts, Vassena, & Silvetti, 2015; Evans, Boggero, & Segerstrom, 2016; but see Inzlicht & Marcora, 2016), but there are only a few experimental studies that directly targeted the commonalities and differences of cognitive and physical effort. One demonstration of their entanglement is offered by Schmidt and colleagues, who showed that the ventral striatum houses a motivational system that drives both cognitive and physical effort exertion (Schmidt, Lebreton, Cléry-Melin, Daunizeau, & Pessiglione, 2012). Another finding is that reward devaluation by cognitive and physical effort correlates with activity in largely overlapping networks of fronto-parietal areas (Chong et al., 2017). These empirical studies are consistent with the idea that common neural mechanisms underlie the motivational aspects of the decision to invest cognitive or physical effort. However, there is also evidence that physical effort is regulated by dopaminergic mechanisms involving nucleus accumbens, while the involvement of these mechanisms is less clear for cognitive effort (Hosking, Floresco, & Winstanley, 2015; Westbrook & Braver, 2015).

The lack of theoretical integration of physical and cognitive effort is peculiar, since in every-day life we often need to decide whether to invest physical or cognitive effort, or both. Putting together an IKEA closet, for example, requires cognitive effort to decipher the instruction, as well as physical effort to actually assemble the closet (along with frustration tolerance when progress is stalled). Depending on cognitive and physical talents, some people may prefer to give instructions to their companion from the sideline, avoiding the physical exercise, while others may prefer to follow instructions, avoiding the cognitive demand. Similar principles are at play when engaging in (team) sports that are both physically and cognitively demanding. For example, playing football obviously requires physical activity, but also cognitive processes such as recalling tactics at appropriate moments, or allocating attention towards relevant aspects of the game (e.g., the ball, the opponent, or team mates).

An explanation for impaired physical performance due to cognitive fatigue is currently missing. It could be argued that opportunity costs accumulate when two effortful tasks have to be performed together or subsequently, even if they are of different modality. Both tasks are probably regarded aversive, since engagement in them precludes the actor from engaging in other, more preferred, activities. However, this explanation does not offer much insight into the exact mechanisms at play.

Unifying cognitive and physical effort under multiple resources theory also seems difficult. Principles of cross talk and parallel processes are hard to apply to physical effort. This is true to an even greater extent for the investment of combined physical and cognitive effort. This would require shared representations between cognitive and physical tasks. One suggestion in that direction has been made by de Morree and Marcora (2015), who propsed that cognitive fatigue directly affects the brain regions involved in the cognitive aspects of physical activity. For example, motor control and cognition seem to converge in dACC, and repeatedly producing a physical force can be cognitively demanding in itself. In that case, the cognitive and physical task might share neuronal pathways. This would explain why a cognitive demanding task increases the effort rating of a subsequent physical task (Marcora, Staiano, & Manning, 2009). Yet, a robust and crystalized theory in accordance with this line of thought is currently lacking. Besides, it seems a bit farfetched to ascribe the experience of physical effort solely to its (often minor) cognitive component.

It has also been suggested that the perception of physical effort emerges from central motor commands sent to active muscles (for a review see de Morree & Marcora, 2015). Central motor commands consist of activity of (pre-)motor cortical areas related to muscle contractions. The essence of the idea is that when muscles become fatigued, increased motor-related cortical activity is required to maintain physical performance. A copy of the increased motor command is sent to somatosensory areas, which gives rise to the perception of physical effort. A recent study claimed a crucial role for supplementary motor area (SMA) in the transfer of this motor command (Zénon, Sidibé, & Olivier, 2015). This study showed that physical effort is perceived as less effortful after disrupting activation of SMA but not primary motor cortex, using transcranial magnetic stimulation (TMS). This finding was consistent across a range of explicit (i.e., rating scales) and implicit measures (e.g., the probability of accepting to replicate a prior effort and pupil size). The authors suggest that physical effort perception is generated by compensatory neural activation (i.e., in SMA) that itself is not involved in muscle control.

This compensatory increased activity of motor-related brain areas bears resemblance to the way increased cortical activity is generally correlated to increased cognitive effort. Repeatedly performing a cognitive or a physical activity may both lead to neuronal adaptation. In the case of cognitive tasks, this may result in decreased signal-to-noise ratio in relevant areas (Müller & Apps, 2019). In the case of physical tasks, this may lead to impairment of the motor neurons that innervate muscle fibers (Potvin & Fuglevand, 2017). Just like cognitive effort investment can be seen as an attempt to overcome a compromised signal in a population of fatigued neurons (cf. chapter 4), physical effort may serve to energize impaired activation of motor neurons. In both cases, perceived effort may arise from increased activity in central brain hubs governing effort investment. Whether these hubs are the same or different across effort types remains on open question.

Relatedly, it has been suggested that in the context of motor control, intrinsic neural noise may be attenuated by the application of control (Manohar et al., 2015). The presence of noise may compromise the computation of a desired motor command. This may be countered by feedback loops that improve the quality of the motor command output by reducing noise during its computation (Manohar, Muhammed, Fallon, & Husain, 2019). Noise-reduction can therefore lead to both quicker and more accurate motor responses, but it is also costly. Although the exact reason why noise-reduction is costly is unclear, it has been proposed that motivation may serve to overcome this cost. The principle is suggested not to be limited to motor control but also applicable to the cognitive domain, where noise reduction may augment the gain of signal over noise, improving decision making. Although it is not directly clear how noise reduction can explain interactions between cognitive and physical effort, it offers a starting point to unify the deployment of effort in the both domains.

Future directions

Although ample research on cognitive effort has been conducted over the past decades, there are still many avenues to explore. Some of them were already touched upon in this Discussion. For example, treating transient and sustained control as the two poles of a continuum may open opportunities for a more accurate classification of between-group, between-subject, and within-subject differences in control modes. Further, the exact way dACC and lPFC engage in the application of control is still debatable. What are their exact roles in the registration of effort cost, motivation, demands, and the execution of control? What does sustained brain activity actually reflect in sustained control: maintenance of task goals, motivation, effort, attention, vigilance, or all of these? Also, it should be further developed what effort costs actually reflect. Are they the consequence of allocating control or are do they serve to ensure efficient learning and processing?

In the sections below, two more concrete avenues for future research on effortful cognitive control are discussed.

Temporal predictability of conflict

Throughout this dissertation, transient control was consistently distinguished from sustained cognitive control. It was argued that these two modes may be considered the ends of a continuum and not two qualitatively distinct phenomena. This implies that many intermediate types of control exist.

Indeed, the CSE can be considered a measure of transient control, since it fluctuates on a trial-by-trial basis. Yet, it is also a continuation of control from the previous to the current trial and therefore sustained. In the current dissertation, transient and sustained control were often equated to reactive and proactive control (Braver, 2012). Hence, in qualitative terms, transient control is a reactive, late-correction mechanism that can be instigated by a cue or stimulus that signals the need for control (e.g., a conflict trial). Sustained control is a proactive, anticipatory, and tonic mechanism, that can be learned through regularities on previous trials. Because sustained, or proactive, control is effortful (Braver, 2012; Chiew & Braver, 2011, 2013; Kalanthroff, Avnit, Henik, Davelaar, & Usher, 2015), a third different control mode may exist that is anticipatory, yet transient. This implies that control can be sustained, which is always anticipatory, or transient. If it is transient, it can be anticipatory or reactive.

To illustrate transient anticipatory control, we return to a task context where a high degree of conflict can be expected (e.g., an MI context). Further, suppose that the temporal presentation of the conflict (i.e., incongruent trial) can also be predicted. This is for example the case when trials are separated by an ITI with a predictable duration. In this case, control settings may be relaxed at the start of the ITI, saving cognitive costs. Towards the end of the ITI, the control setting might ramp up in anticipation of a conflict trial. This transient anticipatory control mode would preserve performance while minimizing cognitive effort. Such a strategy would easily go unnoticed because it is behaviorally indistinguishable from sustained (anticipatory) control. Also note that in chapter 3, this strategy is not viable because the jittered ITI required for event-related fMRI precluded temporal predictions. In addition, the low temporal resolution of fMRI makes it unfit to assess transient anticipatory versus sustained control.

A mechanism comparable to the one proposed here has been demonstrated in the context of a working memory task. Using single-cell recordings in monkeys, working memory activity was shown to ramp up towards the end of a fixed duration ITI, where the monkey could expect the memory probe (Barak, Tsodyks, & Romo, 2010; Watanabe & Funahashi, 2007). Similar mechanisms might be detectable in human subjects, using electro-encephalography (EEG) or magneto-encephalography (MEG) in the context of a cognitive control task. For example, in a task where the next trial is predicted to be a conflict trial (e.g., in an MI block) and the ITI has a fixed duration, the actor can predict the temporal occurrence of the trial. In this case, an increase in theta power or decrease in alpha power towards the end of the ITI can be expected (Cavanagh & Frank, 2014; van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015; van Ede, Niklaus, & Nobre, 2017; van Noordt, Desjardins, Gogo, Tekok-Kilic, & Segalowitz, 2016). This would be an indicator of increased anticipation when conflict is approaching (i.e., transient anticipatory control). In an MI context with variable ITIs, the next trial is also likely to be conflicting but the temporal occurrence of it cannot be predicted. In this case, the actor must remain on guard throughout the complete ITI and apply sustained control, reflected in tonic theta (or absence of alpha) activity throughout the ITI. This option is the last resort, and substantial effort investment can no longer be avoided. In an MC context, no conflict is predicted, so the temporal predictability of a trial is irrelevant. Control will not be prepared (theta activity will be absent during the ITI) but only be reactivated when unexpected conflict is encountered.

Returning to synaptic working memory theory (Stokes, 2015; chapter 3), transient anticipatory control bears resemblance to reactive control, in the sense that the task-goal might be maintained in activity-silent working memory and only has to be reactivated just in time. Different from reactive control, this reactivation occurs right before the conflict trial is expected instead of directly when the conflict trial has been encountered. There is no explicit cue that instigates the reactivation but it could be argued that with fixed ITIs, the elapsed time serves as a cue. An implicit timer is set after completion of each trial, which “reawakens” the actor right before the next trial is presented.

Cortical sensitization

In chapter 4, several ways were suggested in which effort-induced activation of dACC may initiate more efficient processing in populations of task-relevant neurons. Such neural mechanism may compensate for ambiguous perceptual evidence provided by noisy stimuli and may underlie the gain in (or maintenance of) performance that can be achieved through increasing cognitive effort. For example, a state of increased effort may be mirrored in enhanced synchronization of a population of task-relevant neurons (Buschman & Kastner, 2015; Fries, Reynolds, Rorie, & Desimone, 2001). Cognitive effort may also be reflected in aligned oscillations across task-general (e.g., dACC or lPFC) and task-specialized areas. For example, recent computational modeling have demonstrated how synchronization can be used to diminish crosstalk between competing neural areas (Verbeke & Verguts, 2019). Further, cell recordings in monkeys have shown synchrony between prefrontal and parietal cortex through internally controlled attention, where information flowed top-down from prefrontal to parietal cortex (Buschman & Miller, 2007). Likewise, studies using EEG or MEG in humans have demonstrated synchrony between midfrontal and distal cortices following a variety of signals of the need for control. These midfrontal theta oscillations have been extensively linked to controlled processing and are thought to be generated by dACC (for a review see Cavanagh & Frank, 2014). Yet, the exact purpose of neural synchronization in the context of effortful control is still unclear. For example, it remains an open question whether effort-induced synchronized signals indeed sharpen neural precision for processing in task-specialized areas or whether they serve as a simple alarm signal that entrains and overrides operations in these areas (Cavanagh & Frank, 2014).

Another neuronal implementation of increased effort put forward in chapter 4 concerns neuronal noise. Effort investment may initiate a top-down reduction of noise-correlations which leads to an increase of signal-to-noise ratio and a cleaner encoding of task-relevant information (Gilbert & Li, 2013; Ramalingam, McManus, Li, & Gilbert, 2013). Correlations between neurons are difficult to assess in humans but cell recordings in animals have revealed that attention can reduce noise correlations (Cohen & Maunsell, 2009). Recently, it was also suggested that motivation increases precision on a motor task through reduction of noise during computation of the output signal (Manohar et al., 2015, 2019). Although motivation is not effort, the effect of motivation on performance is likely to be exerted through cognitive effort. Despite these examples, it remains speculative if and how top-down effects of effortful control affect noise correlations and signal-to-noise ratios in task-specialized brain. Computational modeling can help to expose more detailed mechanisms.

Conclusion

Taken together, the studies in this dissertation provide three main findings. First, an empirical indicator of time-scale differences in the employment of effortful cognitive control was developed that quantified context-dependent differences in control mode. Cognitive control was shown to operate on a short time scale when conflict is rare and on a long time scale when conflict is frequent. Second, it was shown that these temporal differences in control mode are also reflected in different neural mechanisms. Transient and sustained control were subserved by similar brain areas (i.e., IPS, MFG, and lPFC), but in temporally different neural activity patterns, each with their own effort profile. Finally, the exact neural implementation of cognitive effort was elucidated by demonstrating effort-induced connectivity between dACC and task-specific brain areas. Together, these findings specify the temporal and task-specific profiles of effortful control.

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6

Supplemental material

Data Storage Fact Sheet Chapter 2

% Data Storage Fact Sheet

% Name/identifier study: Chapter 2

% Author: Bart Aben

% Date: 17/01/2020

1. Contact details

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1a. Main researcher

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2. Information about the datasets to which this sheet applies

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* Reference of the publication in which the datasets are reported:

Aben, B., Verguts, T., & Van den Bussche, E. (2017). Beyond trial-by-trial adaptation: A quantification of the time scale of cognitive control. Journal of Experimental Psychology: Human Perception and Performance, 43(3), 1–30. https://doi.org/http://dx.doi.org/10.1037/xhp0000324

* Which datasets in that publication does this sheet apply to?:

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3a. Raw data

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- [ ] research group file server
- [X] other (specify): Research Group Hard Drive at KU Leuven; Open Science Framework (www.osf.io)

* Who has direct access to the raw data (i.e., without intervention of another person)?

- [X] main researcher
- [X] responsible ZAP
- [X] all members of the research group at KU Leuven
- [X] all members of UGent
- [X] other (specify): Anyone with an internet connection.

3b. Other files

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* Which other files have been stored?

- [ ] file(s) describing the transition from raw data to reported results. Specify: ...
- [ ] file(s) containing processed data. Specify:
- [X] file(s) containing analyses. Specify: R script
- [ ] files(s) containing information about informed consent
- [ ] a file specifying legal and ethical provisions
- [ ] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: ...
- [ ] other files. Specify: ...

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  - [X] responsible ZAP

  - [X] all members of the research group at KU Leuven

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Data Storage Fact Sheet Chapter 3

% Data Storage Fact Sheet

% Name/identifier study: Chapter 3

% Author: Bart Aben

% Date: 17/01/2020

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1b. Responsible Staff Member (ZAP)

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2. Information about the datasets to which this sheet applies

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* Reference of the publication in which the datasets are reported:

Aben, B., Calderon, C. B., Van der Cruyssen, L., Picksak, D., Van den Bussche, E., & Verguts, T. (2019). Context-dependent modulation of cognitive control involves different temporal profiles of fronto-parietal activity. NeuroImage, 189(February), 755–762. https://doi.org/10.1016/j.neuroimage.2019.02.004

* Which datasets in that publication does this sheet apply to?:

All data.

3. Information about the files that have been stored

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3a. Raw data

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* Have the raw data been stored by the main researcher? [X] YES / [ ] NO

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- [ ] research group file server
- [X] other (specify): Research Group Hard Drive at KU Leuven; External Hard Drive Main Researcher; OpenNeuro (www.openneuro.org)

* Who has direct access to the raw data (i.e., without intervention of another person)?

- [X] main researcher
- [X] responsible ZAP
- [X] all members of the research group at KU Leuven
- [X] all members of UGent
- [X] other (specify): Anyone with an internet connection.

3b. Other files

----

* Which other files have been stored?

- [X] file(s) describing the transition from raw data to reported results. Specify: data-analysis log
- [X] file(s) containing processed data. Specify: preprocessed fMRI data
- [X] file(s) containing analyses. Specify: Matlab scripts
- [ ] files(s) containing information about informed consent
- [ ] a file specifying legal and ethical provisions
- [ ] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: ...
- [ ] other files. Specify: ...

* On which platform are these other files stored?

  - [X] individual PC
  - [ ] research group file server
  - [X] other (specify): Research Group Hard Drive at KU Leuven

* Who has direct access to these other files (i.e., without intervention of another person)?

  - [X] main researcher
  - [X] responsible ZAP at KU Leuven (Eva Van den Bussche)
  - [X] all members of the research group at KU Leuven
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Data Storage Fact Sheet Chapter 4

% Data Storage Fact Sheet

% Name/identifier study: Chapter 4

% Author: Bart Aben

% Date: 17/01/2020

1. Contact details

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If a response is not received when using the above contact details, please send an email to data.pp@ugent.be or contact Data Management, Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2, 9000 Ghent, Belgium.

2. Information about the datasets to which this sheet applies

===

* Reference of the publication in which the datasets are reported:

Aben, B., Calderon, Van den Bussche, E., & Verguts, T. (submitted). Cognitive effort modulates connectivity between dorsal anterior cingulate cortex and task-relevant cortical areas.

* Which datasets in that publication does this sheet apply to?:

All data.

3. Information about the files that have been stored

===

3a. Raw data

----

* Have the raw data been stored by the main researcher? [X] YES / [ ] NO

If NO, please justify:

* On which platform are the raw data stored?

- [ ] researcher PC

- [ ] research group file server
- [X] other (specify): Research Group Hard Drive at KU Leuven; External Hard Drive Main Researcher
- [X] data will be made available on OpenNeuro (www.openneuro.org) after publication of the study

* Who has direct access to the raw data (i.e., without intervention of another person)?

- [X] main researcher
- [ ] responsible ZAP at KU Leuven (Eva Van den Bussche)
- [X] all members of the research group at KU Leuven
- [ ] all members of UGent
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3b. Other files

----

* Which other files have been stored?

- [X] file(s) describing the transition from raw data to reported results. Specify: data-analysis log
- [X] file(s) containing processed data. Specify: preprocessed fMRI data
- [X] file(s) containing analyses. Specify: Matlab scripts
- [ ] files(s) containing information about informed consent
- [ ] a file specifying legal and ethical provisions
- [ ] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: ...
- [ ] other files. Specify: ...

* On which platform are these other files stored?

- [X] individual PC
- [ ] research group file server
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