Performance monitoring and decision-making: psychophysiological and developmental analyses
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10. Summary and Conclusions

10.1. Introduction

This thesis was concerned with the development of two skills mediated by the ventromedial and dorsolateral prefrontal cortex—two functionally and regionally differentiated regions of the prefrontal cortex. Current models on frontal lobe maturation suggest that functions that rely on the prefrontal cortex develop slowly (Dempster, 1993; Stuss, 1992; Welsh, 2002). This claim is inspired by both biological models showing that the frontal lobes are late to mature (Fuster, 1997; Stuss, 1992), and by the striking similarity between deficits observed in patients with prefrontal damage and the performance of children (Dempster, 1993). Generally, it has been hypothesized that prefrontal maturation is associated with a developmental change in the ability to self-regulate behavior (Posner & Rothbart, 2000).

The functional differentiation between the dorsal and the ventral anatomical pathways (the latter having important reciprocal connections with the limbic structures), reflect dual origins of the frontal cortex (Fuster, 1997). Additionally, different clinical syndromes result from lesions to these pathways. For example, ventromedial prefrontal damage is associated with social impulsivity, whereas dorsolateral prefrontal damage is associated with difficulties in planning and keeping information in working memory. The distinction between these prefrontal cortex functions may especially be important for the development of self-regulation. That is, maturation of the ventromedial prefrontal cortex may be associated with social and emotional aspects of self-regulation (Tucker, Luu & Pribram, 1995), whereas maturation of the dorsolateral prefrontal cortex may be more associated with the cognitive aspects of self-regulation (Stuss, Shallice, Alexander & Picton, 1995).

10.2. Summary

10.2.1. Studies on the functions of the ventromedial prefrontal cortex

Chapters 2 to 4 of this thesis presented studies on decision-making, presumed to be a central function of the ventromedial prefrontal cortex. Damasio's somatic marker hypothesis (1994) provides a unified account of the functions of the ventromedial prefrontal cortex, and holds that emotions play a critical role in human decision-making. When a difficult decision for which future outcomes cannot be easily predicted on the basis of logical cost-benefit comparisons has to be made, people make use of 'somatic markers'. These are mainly emotional responses associated with previously learned outcomes of situations, and the reinstatement of these somatic states becomes important when a resembling decision has to be made. The associations hold the potential to reactivate an emotion by acting on the appropriate cortical or sub-cortical structures. The Iowa Card Gambling Task has been used as a test for assessing somatic markers that are experienced in real-life situations.
Bechara, Damasio, Damasio & Anderson, 1994). That is, the task resembles real-life in the way it utilizes reward, punishment, and uncertainty about future outcomes. The participant’s task is to pick cards from four options; two options are followed by a high reward and, unpredictably, an even higher loss (disadvantageous options) and two other options are followed by a small reward but the unpredictable loss is also small (advantageous options). The participant should learn to differentiate between disadvantageous and advantageous choices. An important aspect of the task is that participants should use the outcome of their decisions to adjust their strategy. Interestingly, previous studies showed that besides immediate somatic responses following reward and loss, intact individuals develop anticipatory somatic ‘warning’ markers preceding disadvantageous choices. This warning signal is missing for patients who have damage to the ventromedial prefrontal region (Bechara, Tranel, Damasio & Damasio, 1996).

The central question of Experiment 2 was to examine which task components of the Iowa Gambling Task are responsible for a disadvantageous performance strategy using heart rate and skin conductance measures as indices of autonomic activity. This question was inspired by reports in the literature showing that poor performers in comparison with good performers have less autonomic responsiveness following punishment outcomes, but also less autonomic activity preceding disadvantageous choices (Bechara & Damasio, 2002). Participants were all healthy young adults in the age range 18 to 25, and the task used was an adapted version of the Iowa Gambling Task, namely the Hungry Donkey Task. We distinguished participants on the basis of their performance in three subgroups, bad performers (participants who only picked from the disadvantageous decks), moderate performers (participants who slowly learned to differentiate between disadvantageous and advantageous choices) and good performers (participants who adopted the advantageous strategy relatively fast). Punishment resulted in heart rate slowing and skin conductance increase, and the magnitude of autonomic responsiveness was positively related to the magnitude of punishment. Most important, this pattern of autonomic activity was similar for bad, moderate and good performers, suggesting that a disadvantageous performance strategy was not related to a failure to process the direct consequences of a performance choice. In contrast, the groups significantly differed in their somatic responsiveness preceding performance choices. Good performers acquired larger skin conductance responses and larger heart rate slowing preceding disadvantageous choices. These results were interpreted suggesting that decision-making impairments in bad performers arise from a weak somatic response generated by secondary inducers (i.e., somatic markers), rather than a weak somatic response generated by primary inducers of reward and punishment (Damasio, 1994; Bechara & Damasio, 2002). In this sense, bad performers resembled patients with ventromedial prefrontal damage.

Chapter 3 examined if children’s performance also resembled performance of patients with ventromedial prefrontal damage, which could be an indication that this region of the prefrontal cortex matures slowly. For this purpose we conducted two experiments. Participants of four age groups (6-9 years, 10-12 years, 13-15 years, 18-25 years) performed the Hungry Donkey Task. The results showed a pronounced developmental increase in the ability to learn to differentiate between disadvantageous and advantageous choices. Given that the task is complex, and several processes are necessary for successful task
completion, we included additional measures that could possibly account for poor gambling performance in young children. Three hypotheses were assessed that might explain developmental changes in decision-making.

First, the deficient performance of children could be due to a stronger orientation towards reward and to their insensitivity to punishment. To examine this possibility, all participants performed two versions of the gambling task; one in which reward was placed up front and punishment was delayed ('standard' version) and one in which punishment was placed upfront and reward was delayed ('reversed' version). On both versions of the task, children preferred options that were immediately advantageous, despite long-term losses. This finding suggests that children were not hypersensitive to reward or insensitive to punishment, rather, they failed to anticipate future outcomes.

Second, it could be that children have difficulties inferring the performance rule ('pick from the low reward options because future outcomes are larger'). To assess this possibility, all individuals completed a standard 'rule induction task', the Raven Progressive Matrices. This task requires individuals to manage problem-solving skills in working memory, and to cope with novelty of a problem. The correlation between Raven scores and gambling performance was non-significant, suggesting that inductive reasoning could not account for developmental changes in decision-making.

Third, it could be that children are unable to keep the outcomes of their choices in working memory. This issue was addressed by presenting different versions of the task in which working memory load was manipulated. This task manipulation did not alter the age effect. In a second experiment including similar age groups we contrasted children's performance on the gambling task with a well-known working-memory task, Digit Span Backwards. Again, the correlation between working memory capacity and gambling performance was non-significant, suggesting that developmental changes in working memory load could not account for the developmental changes in decision-making.

Moreover, in an unpublished study, Crone, Latenstein and Van der Molen (2003) further examined which processes underlie poor decision-making in young children. We designed different versions of the Hungry Donkey Task, using two and four choice tasks that could differ in the frequency with which delayed punishment was presented. The most important results from this study were that children as young as six years old were able to dissociate between disadvantageous and advantageous choices when the delayed punishment was frequent, independent of whether the task included two or four response options. When the delayed punishment was infrequently given (but high in magnitude), children kept preferring the disadvantageous choices, also when there were only two choice options. Together, these results were interpreted suggesting that children's performance resembles that of patients with ventromedial prefrontal damage, and the decision-making impairment is most prominent when there is high uncertainty about future outcomes. This interpretation is consistent with Damasio's somatic marker hypothesis, suggesting that somatic markers are most relevant when the decision-making space is large.

The performance of ventromedial patients is very similar to that of impulsive individuals. In chapter 4 the relation between the trait variable of disinhibition (sensation-seeking) and decision-making was examined. Adolescents of two age groups (12-13 years and 15-16 years) and young adults (18-25 years) were selected on the basis of their disinhibition
score on the Sensation Seeking Scale and completed both the standard and reversed version of the Hungry Donkey Task. Interestingly, disinhibited individuals performed much more disadvantageously on the 'standard' version of the task, but outperformed inhibited individuals on the 'reversed' version. The disadvantageous performance pattern on the standard version of the task is consistent with studies in the literature showing that substance abusers and low-anxious psychopaths (purportedly disinhibited groups) perform disadvantageously on the Iowa Gambling Task (e.g., Grant, Contoreggi & London, 2000; Schmitt, Brinkley & Newman, 1999). The individual differences in ‘trait’ disinhibition could not be accounted for by differences in behavioral disinhibition, as indexed by the Matching Familiar Figures Test. These results were interpreted in the context of Newman's response modulation hypothesis (Newman, Schmitt & Voss, 1997), suggesting that reward induced a dominant approach set that, in high-disinhibited individuals, interfered with the processing of the future consequences of their decisions and prevented them to adjust their performance accordingly. This pattern is not observed when punishment is the salient characteristic. Thus, the apparent failure of high-disinhibited individuals to process the future outcomes of their decisions is secondary to their inability to suspend a dominant approach set induced by rewarded choices.

Given the important relation between disinhibition and the protracted maturation of the frontal lobe in developmental psychology (e.g., Dempster, 1993; Welsh, 2002), a second goal of this chapter was to examine if developmental changes in disinhibition contributed to the changes in decision-making observed with advancing age. Consistent with the performance patterns reported in Chapter 3, adolescents performed better than children in middle childhood but were less risk averse than adult individuals. These results are in accordance with adolescents being less sensitive to the future outcomes of their decisions than adults. Most importantly, developmental changes in gambling performance could not be accounted for by the inability to suspend a dominant approach set induced by reward as seen in cognitively disinhibited individuals.

10.2.2. Studies on the functions of the dorsolateral prefrontal cortex

The dorsolateral prefrontal cortex has often been associated with the supervisory attention system of Norman and Shallice's (1986) model. This area of the prefrontal cortex is known as one of the most important regions responsible for maintaining and manipulating information in working memory (e.g., Kane & Engle, 2002). The classical task that has been associated with dorsolateral prefrontal functioning is the Wisconsin Card Sorting Task (WCST). As stated in the introduction chapter, the WCST is a complex task, requiring several processes for successful performance. Chapters 5 to 8 focused on three important aspects of WCST performance, namely feedback processing, maintaining sorting rules online, and shifting between task sets.

Given that the observations from overt behavior are limited, in Chapters 5 and 6 we used a psychophysiological approach for the study of feedback processing. The ability to monitor one’s behavior was first examined in young adults. Chapter 5 examined heart rate changes associated with positive and negative performance feedback in a probabilistic learning task derived from Holroyd and Coles (2002). An important characteristic of the task is that the stimuli differ in the extent to which performance feedback is informative.
Consistent with previous reports in the literature, when participants prepared for a
response, heart rate slowed, followed by an acceleratory recovery following the response.
The most important finding was that this acceleration was delayed when feedback that
could be used to improve subsequent performance (negative or unexpected feedback) was
given. That is, when feedback was consistently mapped on the left or right response key
(100% condition), negative feedback resulted in heart rate slowing and positive feedback
resulted in heart rate acceleration. In contrast, when feedback was always positive or always
negative (always condition), heart accelerated for both types of feedback. Finally, when
feedback was 50% positive and 50% negative (50% condition), heart rate slowed in both
cases, but the slowing was largest when feedback was different from the previous encoun-
ter. Together, the results indicate that heart rate slowing was elicited when perfor-
ence-based expectations were violated. This slowing was assumed to be associated with a system
that monitors performance-based outcomes for the purpose of future performance adjust-
ments.

In chapter 6, we adopted this approach to examine if children perform worse on
feedback-learning tasks, such as the WCST because of a slowly developing monitoring sys-
tem. For this purpose, the same task was administered to children of two age groups (7-
years, 11-years) and young adults (18-25 years). Heart rate was measured as an index of
feedback evaluation. The results supported the hypothesis that children monitor the out-
come of feedback less efficiently than adults. That is, on a behavioral level, children did not
adjust their performance on the basis of feedback as well as adults. For adults, heart rate
recovery to baseline was delayed following negative feedback when stimuli were consist-
tently mapped onto the left or right key (100% condition) but not when stimuli were
always incorrect (always condition). In contrast, for young children heart rate recovery was
delayed for both types of negative feedback. When feedback alternated on a trial-to-trial
basis (50% condition), young children showed heart rate slowing to all types of feedback,
whereas adults only showed heart rate slowing following feedback that was different from
the previous trial encounters. These findings suggest that all age groups attempted to make
use of the feedback provided to them, but the ability to monitor the relevance of perfor-
mance feedback improves with age. These developmental changes may indicate increased
involvement of the supervisory attention system (Norman & Shallice, 1986).

In Chapter 7, we examined participants' (8-9-year-olds, 11-12-year-olds, 13-15-year-
olds, and young adults) performance on an analogue version of the WCST. Performance
errors were examined on the basis of a recently introduced method of error scoring for the
WCST (Barcelo & Knight, 2002). This method allowed for the differentiation between
ersors due to failure-to-maintain-set (distraction errors) and errors due to failure-to-
t-switch-set (perseverative errors). In one version of the task, the sorting dimension had to
be inferred on the basis of feedback; whereas in a second version, the sorting dimension
was indicated by symbolic task cues on each trial. Results showed that the anticipated age-
related decrease in performance errors was more pronounced for distraction errors than
for perseverative errors. Notably, the presentation of symbolic task cues served to reduce
age-related changes in distraction errors but not in perseverative errors. The apparent dis-
sociation between distraction errors and perseverative errors points to distinct mecha-
nisms that are differentially sensitive to development. More specifically, the developmen-
tal decrease in distraction errors may reflect an increased ability to keep information online (e.g., Case, 1985; 1992), whereas the decrease in perseverative errors is more likely the result of changes in the ability to switch sets (e.g., Zelazo, Frye & Rapus, 1996).

The developmental changes in ability to switch between sets were further examined in Chapter 8. Using the task-switch paradigm, we examined differences in response times between task-repetition and task-alternation. The detrimental effects of changing tasks have been referred to as 'switch costs'. Based on previous studies that showed no changes in developmental switch costs when the endogenously controlled preparation time was manipulated, we tested the hypothesis that children's switch costs may result from more interference due to 'automatic' stimulus-response bindings. Using a theoretical framework proposed by Meiran (2000), we examined switch costs following response repetitions and response alternations in a two-choice task. Children’s switch costs were much larger than those from adults, but only when responses were repeated. When responses were alternated, there was no difference in switch costs between age groups. Developmental changes in task switch costs may therefore be explained in terms of greater involuntary retrieval of stimulus-response associations, which interferes with the ability to switch to currently intended actions (Soetens & Hueting, 1992).

10.2.3 Clinical Application: The interplay between emotion and cognition in ADHD

The last study in this thesis focused on impulsive behavior. A well-known developmental disorder that has been associated with frontal lobe dysfunction is Attention Deficit/Hyperactivity Disorder (Barkley, 1997; Welsh, 2002). Recent reviews of executive function performance in children diagnosed with ADHD indicate a fairly clear pattern of specific deficits, such as difficulties in interference suppression (Barkley, Grodzinsky & DuPaul, 1992; Pennington & Ozonoff, 1996). A second line of research points to deficits mainly in the motivational domain, such as difficulties with processing reward and punishment (Douglas, 1988; Quay, 1997). In Chapter 9 we examined the possible interplay between cognitive and motivational inhibition in children with ADHD and control children. Participants completed a go/nogo flanker task in three conditions, one in which reward was placed upfront, one in which occasional punishment was presented, and a third condition which consisted of an equal number of reward and punishment trials. During the task, heart rate and skin conductance measures were continuously recorded. The results indicated two important findings. First, children with ADHD had a pronounced deficit inhibiting interference from incongruent flankers, consistent with the proposed deficit in the cognitive domain. Second, children with ADHD also were much less accurate when facing punishment than control children, and showed less heart rate differentiation following positive and negative feedback than control children, consistent with the proposed deficit in the motivational domain. Importantly, these aspects of performance ('cognitive' interference suppression and 'motivational' punishment processing) did not interact. This finding is consistent with a recent model proposed by Nigg (2001) suggesting that 'cognitive/executive' inhibition and 'motivational' inhibition exert separate effects on behavior of children with ADHD. We emphasized that to unravel the core deficit of this disorder, future studies should focus on separate contributions of cognition and motivation on performance of children with ADHD.
We examined two aspects of self-regulation development, one associated with emotional and social aspects of self-regulation, purportedly mediated by the ventromedial prefrontal cortex, and one associated with cognitive aspects of self-regulation, purportedly mediated by the dorsolateral prefrontal cortex. Both domains of self-regulation did not reach adult levels of performance until middle childhood, suggesting protracted maturation of brain regions associated with these functions.

Obviously, the parallel proposed between brain maturation and developmental changes in performance on tasks presumed to rely on these regions can be readily criticized. For example, we did not directly measure brain activity, and the studies presented were largely cross-sectional. Nonetheless, physiological measures such as skin conductance and heart rate may provide a more solid basis for relating developmental changes in performance on tasks known to rely on different brain regions and actual brain maturation. For example, in a recently completed unpublished study, Crone, Van der Hal, Van Ommeren and Van der Molen (2003) examined performance of three age groups (7-8 year-olds, 10-12 years-olds and 15-16 years-olds) on the Hungry Donkey decision-making task (as used in Chapters 2 to 4) and the WCST-analogue task (as used in Chapter 7). The same participants performed both tasks while heart rate and skin conductance were continuously recorded. The behavioral results were largely a replication of the results we presented in Chapters 2 to 4 and Chapter 7. Again, performance on the decision-making task did not reach adult level until adolescence, and performance on the WCST-analogue task reached an adult level during middle childhood. Importantly, analysis of physiological responses in the decision-making task revealed that children and adolescents did not differ in autonomic responsiveness following reward and punishment, but the anticipatory responsiveness preceding disadvantageous and advantageous choices was much more diffuse for the youngest age group. These results provide further evidence for the suggested age-related changes in acquiring somatic markers, while somatic responses to primary inducers (reward, punishment) may already have reached mature levels in 7-year-olds. Analysis of heart rate changes following feedback in the WCST-analogue task revealed that children and adolescents showed similar heart rate slowing following the presentation of an external signal (negative feedback) indicating that the previous sorting rule is no longer correct. When making a perseverative error, adolescents' heart rate significantly decreased, indicating that the error was evaluated for the purpose of adjusting future behavior. In contrast, young children did not show such heart rate slowing, suggesting that the system that monitors the need for performance adjustments does not register a perseverative error as such. A tentative interpretation is that the failure to monitor these types of errors may account for the large number of perseverative errors seen in young children.

We suggest that developmental models on prefrontal maturation, originally proposed by Stuss (1992) and Dempster (1993), can be articulated further on the basis of the anatomical differentiation between subregions of the prefrontal cortex. Previous studies examining the development of prefrontal functioning used complex tasks (such as the WCST) and used different measures to describe developmental changes. One of the major virtues of decomposing functions of the prefrontal cortex is that this method may allow assessment of each function in terms of its anatomical basis and psychophysiological
manifestation. The studies described in this thesis illustrate this approach. The task for the future is to gain converging evidence from anatomical, neuropsychological, and psychophysiological (including neuroimaging) analysis that may provide a working model for functional and regional prefrontal segregation and that may account for the developmental changes as well as individual differences in various aspects of self-regulation.