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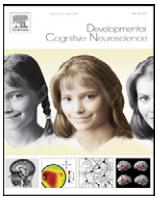

Delayed development of proactive response preparation in adolescents: ERP and EMG evidence

Clare Killikelly*, Dénes Szűcs*

Centre for Neuroscience in Education, Department of Psychology, University of Cambridge, Downing Street, Cambridge, CB2 3EB, United Kingdom

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The transition from late adolescence to young adulthood is often overlooked in the cognitive neuroscience literature. However this is an important developmental period as even older adolescents have not yet reached adult level ability on many cognitive tasks. Adolescents (16–17-year olds) and young adults (23–30-year olds) were tested on a cued task switching paradigm specifically designed to isolate response preparation from response execution. A combined ERP and eletromyographic (EMG) investigation revealed that adolescents have attenuated contingent negative variation (CNV) activity during response preparation followed by larger P3b amplitude and EMG activity in the incorrect response hand during response execution. This is consistent with deficient response preparation and a reactive control strategy. Conversely young adults engaged increased response preparation followed by attenuated P3b activity and early EMG activity in the correct response hand during response execution which indicates a proactive control strategy. Through real time tracking of response-related processing we provide direct evidence of a developmental dissociation between reactive and proactive control. We assert that adoption of a proactive control strategy by adolescents is an important step in the transition to adulthood.

1. Introduction

Impulsivity, lack of foresight, and poor decision-making are trademarks of adolescent behaviour (Crone, 2009; Paus, 2005; Steinberg, 2005). Nevertheless as adolescents transition into adulthood they will need to engage appropriate goal directed behaviour despite distracting complex environments. Currently the neural processes responsible for the transition from immaturity in adolescence to goal-directed behaviour in young adulthood have not been clearly established (Andrews-Hanna et al., 2011). Some research suggests that many of the immature behavioural characteristics of adolescence result from lack of cognitive control i.e. 'the inability to regulate thoughts and actions in accordance with internally represented behavioural goals' (Andrews-Hanna et al., 2011; Braver, 2012; Manzi et al., 2011).

Recently cognitive control has been dissociated into two components; proactive and reactive control (Braver and Gray, 2007; Jacoby, 1999). According to Braver and Gray's Dual Mechanisms of Control model (DMC) (2007) proactive control refers to a preparatory process that can be sustained over the course of the task whereas reactive control is a transient control process that is implemented directly following the perception of a stimulus. Research suggests that adolescents may use a reactive control strategy for completing complex cognitive tasks, whereas young adults have developed a proactive control strategy (Andrews-Hanna et al., 2011; Manzi et al., 2011). The aim of the current study is to determine the neuro-cognitive mechanisms underlying the developmental proactive control from adolescence to young adulthood.

* Corresponding authors. Tel.: +44 01223 767600; fax: +44 01223 767602.
E-mail addresses: ck349@cam.ac.uk (C. Killikelly), ds377@cam.ac.uk (D. Szűcs).

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Importantly, the key difference between reactive and proactive control could lie in differential management of response preparation. According to Aron (2011) the criteria for proactive control have two key elements (1) advance preparation and (2) selective control for a particular response tendency (Aron, 2011). Chen et al. (2010) theorized that the proactive control system affects behaviour by adjusting the threshold for response initiation. For example increased proactive control may be obtained by carefully amending response initiation (e.g. slowing responses). The pre-supplementary motor area (preSMA), the right inferior frontal circuit and the subthalamic nucleus (STN) are found to be involved in both reactive and proactive stopping however, importantly, in proactive stopping this stopping network is pre-activated (Aron, 2011). Therefore the key differences between proactive and reactive control could lie in the temporal activation of preparatory response related processing.

Additionally the developmental course for sustained response control extends into late adolescence (Hämmerer et al., 2010; Ladouceur et al., 2004; Luna et al., 2004a,b; Shing et al., 2010; Williams et al., 1999). An fMRI investigation found that transient (reactive) activation of neural areas supporting inhibitory control decreased from childhood to adolescence whereas sustained (proactive) activation increased in adulthood (Velanova et al., 2009). This perhaps is due to the development of a proactive control strategy. In particular Ordaz et al. (2010) concluded that limitations in adolescents' ability to inhibit a response may be related to fundamental differences invoked to prepare a response.

In order to examine developmental differences in proactive preparation we designed a conditional task switching paradigm that can separate response preparation from response execution. In this paradigm participants are firstly presented with a circle or square visual cue that has been designated at the start of the experiment to indicate that the subsequent trial will most likely be a 'go' trial (press on the same side as the stimulus) or a switch trial (press on the opposite side to the stimulus). Secondly after the circle or square (shape) cue a tone is heard that will indicate either go, switch, or stop responses (Fig. 1). The blocks also included trials of GO cues followed by switch tones (GO/sw) and SWITCH cues followed by go tones (SW/go). This was to ensure that the participants actively engaged control throughout the task and did not come to expect certain stimulus-response patterns. Stop trials were also included to ensure that participants attend to the stimuli and not just the cue. The time between the shape cue and the tone is considered a response preparation phase. Neural differences in proactive response preparation in conditions of low control (GO cue followed by go tone) and high control (Switch cue followed by switch tone) will be compared in this response preparation phase. It is thought that increased proactive control will be engaged during the condition of high control (Switch cue followed by switch tone). The primary aim of this study is to compare the neural activity of adolescents and young adults during the response preparation phase to identify whether or not they use a similar proactive control strategy.

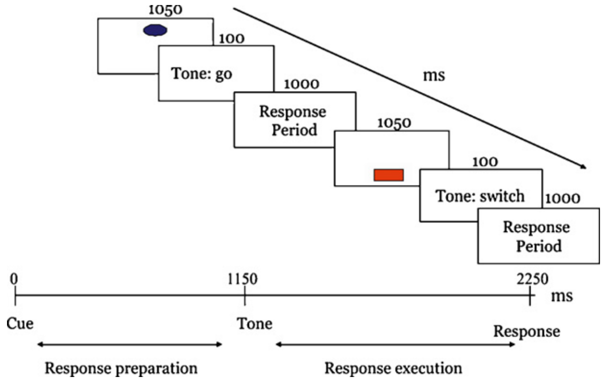

Fig. 1. Schematic of several trials. Participants were told that the blue circle indicates that a go tone will likely follow whereas the red square indicates that a switch tone will likely follow. This was counterbalanced. Response preparation was analysed between 0 and 1150 ms and response execution was analysed between 1150 and 2250 ms after the tone.

To examine preparatory neural activity two ERP components are commonly examined: the lateralized readiness potential (LRP) and the contingent negative variation (CNV). The LRP is thought to represent the initiation of a motor response as it measures the differential activation of electrodes over the left and right motor cortex (C3 and C4 respectively) (Gratton et al., 1988). The LRP can give precise temporal information about the activation of the motor cortex in the context of response hand preparation. The developmental progression of the LRP has been identified in children (Bryce et al., 2011; Ridderinkhof and van der Molen, 1995; Szucs et al., 2009a) however not in adolescents. In terms of childhood development it is found that correct response hand preparation becomes increasingly faster with age (Ridderinkhof and van der Molen, 1995) while early incorrect hand activity during interference decreases with age (Szucs et al., 2009a).

Similarly neural correlates of preparation can be measured using the CNV (Weerts and Lang, 1973). Response activity is normally preceded by an increasingly negative wave over frontal and central electrode cites. This negativity is found to reflect motor preparation for the response (Loveless and Sanford, 1975), sensory anticipation (Gómez et al., 2003) and activation of attentional networks (Fan et al., 2007). Although the CNV is not a direct measure of response-related processing it provides information on preparatory processing. Few studies have examined CNV preparatory activity across development, particularly in a cued task-switching context. However studies involving the No-Go task and a cue-probe task have found either the complete absence of the CNV in children (Flores et al., 2009; Perchet and Garcia-Larrea, 2005) or increasing amplitude with age (Jonkman et al., 2003; Jonkman, 2006). We predict that if adolescents have immature proactive control during the response preparatory phase they will exhibit decreased LRP and CNV amplitude compared with young adults.

As the focus is on response-related aspects of preparation, electromyography (EMG) provides a robust direct measure of motor activity at the level of effectors. Electrodes are placed on each hand and this can record parallel correct and incorrect activity over the course of a task