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Cognitive control and midline theta adjust across multiple timescales

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ABSTRACT

Cognitive control of attention in conflict situations is a basic skill that is vital for goal-oriented behavior. Behavioral evidence shows that conflict control occurs over successive trials as well as longer time scales of trial blocks, but the relation among time scales as well as their neural mechanisms are unclear. This study used measures of behavior, EEG, and a simple quantitative model to test the hypothesis that conflict control at the block level is not exclusively driven by control adjustments over successive trials. Young adults performed an auditory Simon task, and the base rate of compatible vs. incompatible trials was manipulated in separate blocks (25, 50, 75% compatible). EEG data were analyzed using independent component analysis (ICA) to define cortical mechanisms of any base rate and trial-by-trial sequence effects. Reaction time measures had both sequence and base rate effects. Two fronto-medial ICA components indexed sequence and base rate effects, with specific profiles for evoked potentials and oscillations in the theta and alpha frequency bands. Predictive modeling showed that sequence effects accounted for a minority of the variance on behavioral and ICA measures (all < 36%). The results strongly suggest that the base rate manipulation affected behavior and many neural measures beyond the influence of sequence effects.

1. Introduction

The ability to pursue and achieve goals is vital for intelligent behavior. Setting attentional biases to promote goal attainment is a basic process in cognitive control (Miller and Cohen, 2001). Nonetheless, task-irrelevant information still influences performance, and when performance suffers this is termed a “conflict” between relevant and irrelevant information (Botvinick et al., 2001). The Stroop, Flanker, and Simon tasks are commonly used to study cognitive conflict (Eriksen and Eriksen, 1974; Simon and Rudell, 1967; Stroop, 1935). The specific nature of the conflict varies in the three tasks, but all are thought to generally involve conflict that arises during the response selection stage (Egner, 2017).

The Simon task indexes the degree that irrelevant spatial information captures attention (Simon and Rudell, 1967). Subjects respond using the left or right hand on the basis of a non-spatial stimulus feature, such as pitch. Performance in the Simon task is better when the hand and sound location are on the same side (compatible trials) relative to having different locations (incompatible trials). The degree of conflict is quantified by differences in reaction time and accuracy among compatible versus incompatible trials (termed the “Simon effect”). Spatial hearing has particular ecological importance as an early warning system (Hartmann, 1999; Scharf, 1998). Potent attention capture in spatial hearing may be why, as compared to vision, the auditory Simon effect is usually larger (Vu et al., 2003) and evident across a wider range of reaction times (Wascher et al., 2001).

The degree of conflict on the time scale of minutes can be manipulated by varying the base rates of compatible and incompatible trials within an entire block of trials (Stürmer et al., 2002); also termed “list-wide proportion congruence” (Logan and Zbrodoff, 1979). For simplicity, here we use the term base rate. The basic result is that the conflict effect increases with the base rate of compatible trials (reviewed in Bugg and Crump, 2012). Base rate effects are often characterized as an indication of cognitive control strategy (e.g. Risko et al., 2008). Participants may decrease cognitive control bias if compatible trials are frequent because it is redundant with location information. Thus, in the Simon task compatible trials may reinforce the tendency to respond with the hand that matches stimulus location, and incompatible trials may serve as a reminder to try to ignore spatial information. Therefore, trial blocks with mostly compatible trials have fewer reminders and larger Simon effects. This explanation fits in with a Dual Mechanisms Framework for cognitive control in which

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participants activate “proactive control” to set attentional biases in anticipation of conflict for the next stimulus (Braver, 2012). Other researchers have also explained the base rate effect as being caused by a strengthening of correct stimulus-response associations with decreasing compatible trial base rate (Cao et al., 2017).

Cognitive control has also been examined on the shorter time frame of successive trials (Egner, 2007; Gratton et al., 1992; Larson et al., 2009; Wühr and Ansorge, 2005). Results show that the Simon Effect is smaller on the trial after an incompatible trial, relative to having a previous compatible trial (Gratton et al., 1992). These “sequence effects” may be due to a system that monitors for conflict in response selection. When conflict exceeds a threshold cognitive control would then enhance task-related biases on the next trial (Botvinick et al., 2001). These trial-by-trial adjustments may map onto the idea of “reactive control” in which participants respond to stimuli across shorter timescales rather than proactively adjusting control across longer periods of time (Braver, 2012). Proactive and reactive control are not necessarily exclusive of each other, and some researchers have suggested that anticipatory proactive control can adjust on shorter timescales as well (van Driel et al., 2015). It is therefore possible that with sequence effects participants are proactively adjusting attention on a trial-by-trial basis as a function of the previous trial type.

Base rate and sequence effects are interrelated because the proportion of each type of sequence covaries with base rate. The higher the proportion of compatible trials, the greater the chance that for any given trial the previous trial was compatible. Since there is a larger Simon effect following compatible trials, it must also be the case that blocks with higher compatible base rates (and thus more trials preceded by compatible trials) will have larger Simon effects. It is even possible that sequence effects could entirely drive base rate effects. Nonetheless, researchers often study base rate effects without considering sequence effects. An exception is Risko et al. (2008), who found that controlling for the specific sequences of stimulus and response locations across pairs of trials reduced the base rate effect by 47%. In another study Torres-Quesada et al. (2014) found that base rate effects were present when compatibility sequence effects were absent. Together these results suggest that base rate effects on longer time scales are only partially driven by sequence effects on short time scales.

The issue of how sequence effects relate to base rate effects can also be approached by including measures of neural activity (e.g. Cieslik et al., 2015; Larson and Lee, 2014). The anterior cingulate cortex (ACC) has been implicated in cognitive control in fMRI (Kerns et al., 2004), EEG (van Veen and Carter, 2002), and lesion studies (di Pellegrino et al., 2007). Kerns (2006) found that the ACC was involved in detecting and responding to Simon task conflict, and that ACC activity then predicted prefrontal cortex activity on the next trial. This finding supports a conflict-monitoring hypothesis in which the ACC monitors conflict and then signals to other brain areas, such as the dorsolateral prefrontal cortex, to help deal with conflict on upcoming trials (Botvinick et al., 2004; Kerns, 2006). These findings highlight the importance of frontal midline areas in modulating cognitive conflict, and provide a foundation to test how well neural mechanisms of sequence effects can account for base rate effects. On the other hand, some researchers have suggested that the ACC does not monitor conflict (Burle et al., 2008). The current study aimed to clarify this issue by looking at neural activity during conflict across multiple timescales.

Frontal event-related potentials (ERPs) and EEG oscillations that index conflict, in particular the theta band, likely reflect activity in the same medial frontal brain areas previously implicated in cognitive control (Gevins et al., 1997; Kerns, 2006). For example, Hanslmayr et al. (2008) used source localization to find that a conflict-sensitive ERP and frontal theta during a Stroop task both originated in the ACC. ERP components known as the "N2" in Flanker tasks (Clayson and Larson, 2011) or as the “N450” or “medial frontal negativity” (MFN) in Stroop or other conflict tasks are larger (more negative) for incompatible versus compatible trials, and are thought to originate in the ACC (Larson et al., 2009; West and Bailey, 2012). The MFN/N450 peaks at ~ 450 ms in visual Stroop tasks (Tillman and Wiens, 2011; West and Bailey, 2012). It shows both base rate and sequence effects, and is thought to reflect conflict monitoring (Cespón et al., 2016; Larson et al., 2009; West and Bailey, 2012). Also in Stroop tasks, the amplitude of a subsequent component called the “frontal slow wave” (latency ~ 600 to 800 ms or later) is also sensitive to conflict and base rate (Bailey et al., 2010; West and Bailey, 2012). The medial frontal negativity occurs before a response is made and is likely related to conflict detection and processing. Because the frontal slow wave occurs after the average response time, it may reflect across-trial adaptations such as increases in proactive conflict monitoring or between-trial processes such as updating working memory (West et al., 2012).

Neural oscillations have also implicated frontal and midline brain areas such as the ACC in cognitive control (Buzsaki and Draguhn, 2004; Cohen and Ridderinkhof, 2013; Cohen et al., 2008). Increases in power following a stimulus indicate synchronized cortical activity in response to the stimulus, and decreases indicate desynchronization (Pfurtscheller and Lopes da Silva, 1999). Theta power (4–8 Hz) in prefrontal brain areas increases during conflict (Cavanagh and Frank, 2014; Cohen and Cavanagh, 2011; Gulbinaite et al., 2014). In an auditory Stroop task Oehrn et al. (2014) found higher theta power in the dorsomedial prefrontal cortex during conflict, as measured using electrocorticography. Frontal and parietal theta power in the visual Simon task exhibits sequence effects, with a larger Simon effect for the trials after a compatible trial (Gulbinaite et al., 2014; Tang et al., 2013; Töllner et al., 2017). Thus, both behavioral and neural measures of cognitive control adjust on long and short timescales in the Simon task, but to date no study has defined similarities and differences in conflict processing on these two time scales.

The current study had two main purposes. First, we defined the impact of manipulating the base rate of compatible trials on auditory cortical potentials (ERPs and event-related spectral perturbations/ERSPs) identified using independent component analysis (ICA). We hypothesized that a subset of the independent components would be strongly modulated by base rate, and would likely reflect frontal midline areas (anterior cingulate cortex, medial prefrontal cortex) that are associated with cognitive control. Most EEG studies on cognitive conflict have analyzed ERP data at the channel level. The current study used independent component analysis to further examine functionally distinct, independent components of neuroelectric activity at the scalp. The second, and main, objective was to determine if behavior and the components modulated by base rate reflect a genuine effect of base rate. The null hypothesis was that base rate effects on behavior and independent component activity are accounted for by sequence effects, which have been shown to be reduced in patients with anterior cingulate lesions (di Pellegrino et al., 2007). We developed a quantitative model to predict what the base rate effects would be for each participant if they were driven solely by that participant's observed sequence effects. We then compared the predicted base rate effects to the observed base rate effects. Rejection of the null model based on two-trial sequence effects would imply a separate process for adjustment of cognitive control across longer timescales.

2. Method

2.1. Subjects

Fifty-seven subjects were recruited from a University community in exchange for extra credit (mean age = 20.1 ± 2.5 years, 19 males, 2 left-handed). None reported a history of major neurological or psychiatric disorders. Normal hearing thresholds were verified for all subjects with audiometric testing (.5–8.0 kHz). A subset of subjects (n = 35) completed additional cognitive tests and surveys not presented here, including two working memory capacity tests and a questionnaire about musical experience. All subjects were given a handedness