Neural Basis of Implicit Sense of Agency in the Transition from Adolescence to Adulthood

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Abstract

Everyday voluntary actions are accompanied by an intrinsic feeling that we are in control of our actions and their outcomes. The current thesis investigated the brain mechanisms and development of this feeling of agency by focusing on perceived temporal relationship between voluntary actions and their outcomes. It used two phenomena that are central to SoA: temporal recalibration and intentional binding. The results add to the current knowledge by showing the sensory cortical involvement in temporal recalibration (Chapter 2), the developmental trajectory of intentional binding from childhood to adulthood (Chapter 3) and neural correlates of intentional binding from adolescence to adulthood (Chapter 4). The first study revealed that, temporal recalibration, a delay compensation process, can be modulated by a non-invasive brain stimulation technique and sensory specific cortical regions might be at play when the brain is regulating the temporal link between actions and outcomes. Then, taking a developmental approach, the second study revealed a U-shaped developmental trajectory for implicit SoA as indexed by intentional binding from childhood to adulthood, and it was lowest in late-adolescence. These findings suggest that adolescence, a period where final and key maturational changes in the brain observed, is an important period for SoA development. The third study, which investigated intentional binding from adolescence to adulthood using brain imaging (EEG), revealed that mid-adolescents show greater intentional binding and greater P2 attenuation compared to adults, both of which becomes adult-like during late-adolescence. Findings suggested a greater agency experience, which may be mediated by a neural over-attenuation (P2) of action outcomes and over-reliance on motor preparation (late readiness potential) in mid-adolescents, and this became adult-like in late-adolescence. There were intentional binding differences in adults across studies which might be related to different temporal contiguity levels across studies and should be further investigated. Overall, this doctoral work provided novel findings for understanding the neural basis and development of SoA from adolescence to adulthood.

Declaration

This thesis consists of original work that has not been presented for an award at this, or any other university. This thesis was completed by the candidate supervised by Dr. Liat Levita and Dr. Robert Schmidt, except that the work that is presented in Chapter 2 was supervised by Dr. Kwang-Hyuk Lee and Dr. James Stone.

The following publication is based on the work undertaken in Chapter 2:

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Chapter 1

1. Introduction

We are agents who manipulate the external world through our actions in accordance with our internal desires. When we bring about effects in the environment we usually have this intrinsic feeling of being the agent. This subjective experience of being the agent of our voluntary actions and their outcomes has been described as 'sense of agency' (SoA) (Gallagher, 2000; Haggard, 2017; Pacherie, 2008). Agency and its experience are fundamental for human behaviour and everything that has been made by humans, from stone tools to spacecrafts. SoA is also thought to be important when determining responsibility over the outcomes of actions in societal and legal systems (Frith, 2014; Moretto, Walsh, & Haggard, 2011). Furthermore, impairments in SoA can influence our view of reality and functionality as seen in control delusions of schizophrenia (Frith, Blakemore, & Wolpert, 2000; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010; Voss, Chambon, Wenke, Kühn, & Haggard, 2017) as well as in alien limb and apraxia (Wolpe et al., 2014).

SoA has been proposed to have two distinct constituents: judgement of agency and feeling of agency (Synofzik, Vosgerau, & Newen, 2008). Judgement of agency is higher level evaluation of agency. It is important in the situations when we make an explicit attribution of agency. Judgement of agency is associated with processing of higher level information such as belief stances and contextual information about the agency. Feeling of agency, on the other hand is a lower level, pre-reflective background feeling of being an agent. It is associated with processing of lower-level flow of sensorimotor information. Studies of SoA typically investigate these two distinct constituents of agency by using explicit and implicit measures of SoA (Discussed further in section 1.3). Briefly, explicit measures focus on the self-reports regarding participants' judgements about whether they were the agent or judgements about to what extent they felt in control. On the other hand, implicit measures (e.g. intentional binding and sensory attenuation) focus on correlates of voluntary action processes that are sensitive to agency and they infer the experienced agency based on these measures without asking anything about agentic experiences (Moore, 2016).

Despite its vital role in human life, research interest into SoA has only started to increase about two decades ago mostly as a result of significant improvements in measuring SoA (Moore & Obhi, 2012). Although current research has remarkably increased our knowledge, the brain mechanisms and neural correlates of SoA have not been fully elucidated, especially during development. There are still important unanswered questions about SoA as individuals move from childhood to adulthood. For instance, when does it start to become adult-like? Do children and adolescents use cognitive processes and brain mechanisms in the same way adults do when constructing their experiences of agency? How do structural and functional changes in the brain during development affect SoA? What is the functional significance of SoA at different developmental stages? A developmental perspective of SoA, therefore, is necessary for a complete understanding of mechanisms of it as well as understanding human development and behaviour.

The aim of this thesis is, as an attempt to fill this knowledge gap, to investigate the brain mechanisms and development of SoA in the transition from childhood to adulthood with a focus on adolescence using a non-invasive brain stimulation technique (transcranial Direct Current Stimulation: tDCS), electroencephalogram (EEG) and developmental perspective. To that end, the research presented in this thesis focuses on two phenomena that emerge from action-outcome temporal relationship and central to the SoA: temporal recalibration and intentional binding (Haggard, Clark, & Kalogeras, 2002; Stetson, Cui, Montague, & Eagleman, 2006; Timm, Schonwiesner, SanMiguel, & Schroger, 2014; Walsh & Haggard, 2013). The results from these empirical studies will add to the current knowledge by showing the sensory cortical involvement in temporal recalibration, the developmental trajectory of intentional binding from childhood to adulthood as measured by two different methods and neural correlates of intentional binding during the transition from adolescence to adulthood. Before presenting the empirical chapters, I will first start with an overview of the literature that leads up to the research questions of the empirical work undertaken in this thesis.

1.1 Time, Causality and Sense of Agency

The temporal relationship between actions and outcomes is an important indicator of causality and SoA. One determinant of causality is temporal contiguity (Hume, 1739). That is the more two events are close in time, the more they are likely to be perceived causally related (Gruber, Fink, & Damm, 1957; Leslie, 1982; Michotte, 1963). In his seminal experiments, Michotte (1963) showed that a moving object that contacts with a stationary object can be perceived as the cause of the second object's motion. Critically, this only occurred in a condition when there was no delay between first object's contact and second object's movement. However, when a delay was inserted between these two events, the perceived causal relation between first object's contact and second object's motion was reduced. Similarly, perceived causal relationship between action and its outcome is also dependent on the temporal contiguity. That is increasing temporal delay between actions and outcomes decreases the likelihood of an action being judged as the cause of the outcome (Dickinson, 2001; Shanks, Pearson, & Dickinson, 1989). This can also be seen in agency judgements where we are less likely to attribute self-agency for the events that are temporally distant to our actions (Walsh & Haggard, 2013) as well as in the implicit measures of SoA (Blakemore, Frith, & Wolpert, 1999; Haggard et al., 2002).

Notably, recent research has also shown that how we perceive the temporal relationship between two inter-related events including action and outcome is malleable (Buehner & Humphreys, 2009; Fujisaki, Shimojo, Kashino, & Nishida, 2004; Haggard et al., 2002; Stetson et al., 2006). For instance, when there is a consistent delay between actions and sensory outcomes, our brain re-adjusts the perceived time between them to meet the prior expectation that outcomes will follow actions with almost no delay (Stetson et al., 2006). This phenomenon was called temporal recalibration, and suggested to facilitate the causal relationship between events by compensating the delay in between (discussed further in section 1.2). Hence, we can establish a stronger causal link and SoA between actions and outcomes even though they are separated in time with delay (in sub-second range) by recalibrating our perception of time. Interestingly, changes in the recalibrated time perception can affect SoA in a different way as well. That is when the adapted delay is removed after temporal recalibration, the outcome was perceived as preceding the action even though it was not the case in reality. This illusory reversal of temporal order was shown to change subjective agency judgements where participants reported no-agency since they believed that the outcome preceded their own action (Timm et al., 2014). This suggests that adaptation to a new temporal relationship can lead to a re-adjustment in our perception of time; violating this learned relationship by removing the adapted delay can lead to an illusory violation of another important causality rule which is outcomes must follow actions; this consequently leads to a breakdown in our SoA.

The changes in the perceived temporal relationship between actions and outcomes can also be observed without a delay adaptation. That is our voluntary actions can shape the perception of time between actions and outcomes. When voluntary actions and outcomes are coupled, actions are perceived to be happening later and outcomes are perceived to be happening earlier than when they occur alone (Haggard et al., 2002). In other words, there is a perceived temporal compression between action and outcome that binds actions and their external outcomes in time. This phenomenon has been conventionally called intentional binding and is considered as an implicit measure of SoA since it is specific to the voluntary actions and it was not observed when the actions are involuntary (i.e, when an action was triggered by stimulating the motor area with transcranial magnetic stimulation: TMS) (Moore & Obhi, 2012). Furthermore, it has been shown that voluntary actions and causality are prerequisites of intentional binding (Cravo, Claessens, & Baldo, 2009). Hence, intentional binding refers to the effect of agency on the perceived action-outcome temporal relationship (discussed further in section 1.3.1).

As discussed above, action-outcome temporal relations can influence causality perception and SoA; likewise, causality perception and SoA can influence action-outcome temporal relations suggesting a bidirectional relationship. Taken together; 1) temporal contiguity between actions and outcomes is informative about their causal link, 2) temporal recalibration can facilitate the action outcome causality and consequently SoA, 3) SoA can influence the perception of time as seen in intentional binding and it has been widely used as an implicit SoA measure (Moore & Obhi, 2012). Therefore, action-outcome temporal relations are central to the SoA and important to study for a complete understanding of SoA.

In the following sections I will start with introducing sensorimotor temporal recalibration literature that led to the empirical studies presented in Chapter 2 (section 1.2). Then, I will continue with introducing implicit SoA and its measures (section 1.3), mechanisms and brain areas underlying it (section 1.4 and 1.5) and their change from childhood to adulthood (section 1.6), which led to the empirical studies presented in Chapter 3 and Chapter 4. And finally, an outline of the thesis which describes the empirical studies undertaken in each chapter will be presented (section 1.7).

1.2 Sensorimotor Temporal recalibration

Determining a causal link between two stimuli is not a trivial task for the brain. This is because multisensory information that is coming from the same event reaches our sensory receptors at different times, as for example, light travels faster than sound. When the distance of the source is increased, these differential speeds can lead to even more temporal asynchrony. Even if the visual and auditory information reaches us at the same time, it has been shown that they are processed at different speeds by the brain. That is auditory information is processed faster than the visual as seen in simple reaction time tasks where auditory reaction time shown to be about 50 seconds faster than visual (Shelton & Kumar, 2010). Hence, temporal information of these two stimuli, even though they are coming from the same source, is in almost constant flux due to environmental factors (e.g., distance) and neural processing demands. However, we usually perceive them as occurring simultaneously and causally linked. This means our brain is making a constant effort to compensate for these changing asynchronies to overcome this problem. Fujisaki et al. (2004) for the first time showed that the brain might be solving this problem by actively recalibrating the subjective simultaneity (temporal gap in which two stimuli are being perceived as simultaneous) of different modalities. They showed that when an auditory stimulus repeatedly followed a visual stimulus with a constant delay, participants' point of subjective simultaneity (PSS: the time point at which two stimuli are perceived as occurring at the same time) shifted towards the inserted delay. Therefore, this shift in point of subjective simultaneity can help to perceive these two asynchronous stimuli as simultaneous and causally linked. Hence, temporal recalibration is the subjective realignment of inter-related asynchronous signals after a delay adaptation by reducing the subjective time difference between them (Fujisaki et al., 2004; Stetson et al., 2006).

In addition to sensory-sensory (e.g., auditory – visual) pairs, temporal recalibration also occurs between actions and their sensory consequences (sensorimotor temporal recalibration). Stetson et al. (2006) showed that when a constant small delay (e.g., 150 ms) was inserted between action (button press) and its consequent visual outcome (a flash), the point of subjective simultaneity shifted in the direction of the delayed visual outcome which produced a subjective compression of time to compensate for the delay and keep action and outcome causally linked. The effect of the shift in point of subjective simultaneity was seen when this delay was removed. When the artificially inserted delay was removed, participants this time perceived the outcomes as occurring before their action even though the outcomes were still following the action. It was suggested that this adaptation effect occurred as a result of prior expectation that outcomes should follow actions with almost no delay. Following studies showed that, in addition to motor-visual, sensorimotor temporal recalibration can also be observed between motor-auditory and motor-tactile pairs suggesting it might be a central operation of the brain (Heron, Hanson, & Whitaker, 2009; Sugano, Keetels, & Vroomen, 2010, 2012).

The most salient characteristics of sensorimotor temporal recalibration are its strength compared to sensory-sensory temporal recalibration and its dependence on temporal contiguity. Stetson et al. (2006) found that the magnitude of temporal recalibration effect was greatly reduced and illusory reversals of temporal order (outcomes preceding action) did not occur when tactile-visual stimuli pairs were used instead of motor-visual stimulus pairs. This finding highlights the importance of the voluntary action and motor processes in sensorimotor temporal recalibration suggesting an active interaction with the external world may be an important underlying feature of temporal recalibration. In addition, the temporal recalibration effect has been found to be decrease with increasing delay durations; and it even diminished when the delay was extended to 1000 ms (Heron et al., 2009; Stetson et al., 2006). This suggests a strong relationship between temporal recalibration and causality since diminishing causal relationship by increasing the delay has an important consequence on temporal recalibration effect.

Taken together, these two characteristics of sensorimotor temporal recalibration, dependence on voluntary action and temporal contiguity, suggests that sensorimotor temporal recalibration might have strong relationship with sense of agency. For instance, it was previously found that participants' implicit SoA as measured by intentional binding on the test period was dependent on the learned action outcome temporal relationship in the delay adaptation period (temporal recalibration) (Walsh & Haggard, 2013). Furthermore, it was shown in another study that, following temporal recalibration, illusory reversals of temporal order can lead to illusory lack of agency where participants were actually the agent (Timm et al., 2014). Hence, temporal recalibration can help maintaining an experience of agency between actions and their delayed outcomes by establishing a new action-outcome temporal relation and also disruptions to newly established temporal relation (e.g., removing the delay) can affect our perception of temporal order and consequently SoA. Since the attribution of causality and self-agency are impaired in some mental health problems such as schizophrenia (Frith, 2005; Jeannerod, 2009), understanding brain mechanisms of sensorimotor temporal recalibration can lead to a better understanding of these mental problems as well as how the brain constructs an experience of agency.

Although sensorimotor temporal recalibration seems to be a fundamental operation of the brain, its underlying mechanisms are not well understood since there are few studies addressing this issue. Initially a supramodal mechanism which transcends the modality specific brain areas was suggested by Heron et al. (2009) since sensorimotor temporal recalibration was similar for all the modalities (motor-visual, motor-auditory and motor-tactile pairs) and it could be transferred between modalities. In that study, they showed that, even though the delay adaptation was in one modality, it had temporal recalibration effect on another modality. That is adaptation to a delay between action and its visual outcome can have similar temporal recalibration effects on action and its auditory outcome and vice versa. Based on this, they suggested a central mechanism governing sensorimotor temporal recalibration that is above the sensory specific brain areas. Similarly, Sugano et al. (2010) found this transference of temporal recalibration effect across modalities replicating Heron et al. (2009)'s findings. However, they suggested this could be because of a subjective temporal shift in the motor component of motor-sensory pairs so that it is reflected in all modalities. That is, if temporal recalibration is caused by a subjective temporal shift in motor component (action), then temporal recalibration can similarly be observed regardless of the modality of the outcome.

In contrast, there have been findings that are difficult to reconcile with supramodal mechanism (Sugano et al., 2012; Sugano, Keetels, & Vroomen, 2014; Yarrow, Sverdrup-Stueland, Roseboom, & Arnold, 2013) or motor component shift account (Sugano et al., 2012; Sugano, Keetels, & Vroomen, 2016). In a later study, for instance, Sugano et al. (2012) used sensorimotor synchronisation task to measure temporal recalibration effect and to investigate the transference of temporal recalibration (Figure 1.1). Sensorimotor synchronisation task requires participants to tap in synchrony with a regular rhythmic stimulus, which can eliminate high level judgement processes and possible response biases that might be observed in judgement based tasks (e.g., temporal order judgement task, Heron et al. 2009). In this task participants' taps typically precede the rhythmic stimulus which is referred as negative mean asynchrony (Repp, 2005; Repp & Su, 2013). This asynchrony is considered as participants' subjective impression of synchrony between their tap and stimulus (Aschersleben, 2002). In other words, participants need this temporal asynchrony between their tap and pacing stimulus to perceive their tap and pacing stimulus as simultaneous. Participants' negative mean asynchronies before and after a delay adaptation can reveal the changes in the participants' simultaneity perception and show the temporal recalibration effect (further explained in Chapter 2). They showed that sensorimotor synchronisation task can be successfully used to measure temporal recalibration. Interestingly, when they investigated the transference of temporal recalibration between modalities by using different modality in the delay adaptation period and sensorimotor synchronisation period, they found that delay adaptation in visual modality can create similar temporal recalibration effect in auditory modality but not vice versa. This suggests that visual temporal recalibration effect can transfer to auditory modality but auditory temporal recalibration effect cannot transfer to visual modality.

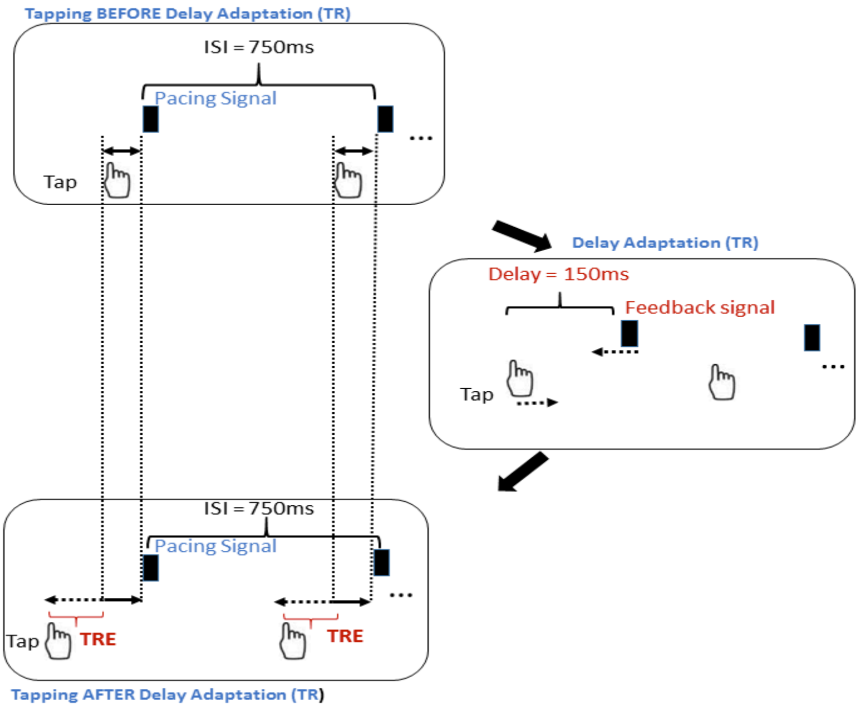

Figure 1.1 *Illustration of sensorimotor synchronisation task for measuring temporal recalibration effect (TRE).* ***Tapping before delay adaptation:*** *Participants tap in synchrony with a regularly pacing stimulus. On average participants tap earlier than the stimulus and it is called Negative Mean Asynchrony (NMA). It represents the participants' subjective reflection of synchrony.* ***Delay adaptation:*** *Then, during delay adaptation period participants press a button regularly and this time receive a 150 ms delayed feedback.* ***Tapping after delay adaptation:*** *After delay adaptation period, participants tap in synchrony with a pacing stimulus again. This time they tap even earlier which increases their NMA. Temporal recalibration effect is calculated as the difference between participants NMAs before and after delay adaptation.*

Sugano and his collegues' (2012) finding challenges the supramodal mechanism and motor component shift idea since if either was the case we would expect to see a similar transference between modalities. In contrast, it suggests that modality specific mechanisms might be involved in temporal recalibration. One possible explanation for this differential transference is that visual timing information might be encoded in auditory representation leading to a temporal recalibration effect transference from the visual to the auditory modality, but auditory timing information might not be transferred to the visual system leading to no transference of temporal recalibration effect to visual modality. This suggests a critical role for the auditory system in cross-modal temporal processing. This idea is in line with the literature suggesting that auditory system is dominant in temporal processing compared to visual system (see Grondin, 2010 for a review). For instance, modality independent role of the auditory cortex was shown in a transcranial magnetic stimulation (TMS) study where auditory cortex stimulation decreased temporal estimation performance to the same degree both in auditory and visual modalities (Kanai, Lloyd, Bueti, & Walsh, 2011). Hence, auditory cortex might be regulating the temporal recalibration regardless of the stimulus modality. However, this hypothesis and the contribution of the modality specific brain areas (auditory and visual cortices) to the sensorimotor temporal recalibration has not been tested before. Therefore, in the present thesis I first investigated the role of the sensory cortical involvement both in auditory and visual domains and possible amodal role of auditory cortex in sensorimotor temporal recalibration. The results from this investigation can help to better understand the brain mechanisms of temporal recalibration and consequently how the delayed action outcomes are processed in the brain to create a unified perception of causally linked events and SoA.

This section presented an overall picture of the sensorimotor temporal recalibration literature that led to the studies in Chapter 2. In the following sections, I will introduce intentional binding and sensory attenuation which have been considered as implicit measures of sense of agency and studied in Chapter 3 and Chapter 4 developmentally.

1.3 Implicit Measures of Sense of Agency

An important theoretical distinction between two components of agency, judgements of agency and feeling of agency, was made by Synofzik, Vosgerau and Newen (2008). Judgement of agency is a higher level cognitive evaluation of agency on one’s action and it occurs in the situations when we make explicit attributions of agency to ourselves or others. Feeling of agency, on the other hand, is a lower level, pre-reflective background feeling of being an agent and we are not necessarily aware of this feeling unless it is disrupted. Judgement of agency is associated with processing of higher level information such as belief stances and contextual information about the agency, whereas feeling of agency is associated with processing of lower level flow of sensorimotor information (Synofzik et al., 2008). Studies of SoA typically investigate these two distinct constituents of agency by using explicit and implicit measures of sense of agency (Haggard, 2017; Moore & Obhi, 2012; Synofzik et al., 2008; Synofzik, Vosgerau, & Voss, 2013).

Explicit measures focus on the self-reports regarding participants' judgement of agency. They involve interpretive explicit judgements about whether participants themselves caused an event to occur or judgements about to what extent they felt in control while their actions causing an event (Aarts, Custers, & Wegner, 2005; Metcalfe, Teal, Eich, & Miele, 2013; Sato & Yasuda, 2005; Timm et al., 2014; Wegner & Wheatley, 1999). These tasks usually include temporo-spatial distortions or congruency manipulations between the actual action and its video feedback or its outcome. Then, participants are asked to report whether they were the agent or to rate their experience of agency on a scale. For example, in an explicit SoA experiment, participants were required to hit a moving target on the screen by using the mouse cursor while avoiding the others (Metcalfe, Eich, & Castel, 2010). When participants tried to hit the target, in some trials the movement of the cursor was delayed, random noise was introduced to the spatial position of the cursor or cursors' radius was increased. Then participants were asked to rate their experience of control on a linear sliding scale from complete control to no control. Although explicit SoA studies provide direct reflections of agency experience, they can be vulnerable to demand characteristics, open to metacognitive confounding factors (e.g., impairments in decision making) or cognitive biases such as overestimating self-agency (Haggard, 2017; Wolpe & Rowe, 2014) and can be difficult to obtain reliably in special populations such as patients (Wolpe & Rowe, 2014).

Implicit measures, on the other hand, focus on correlates of voluntary action processes that are sensitive to agency and they infer the experienced agency based on these measures (Moore, 2016). These measures aim to quantify the feeling of agency that accompanies voluntary actions (Haggard, 2017) by measuring the effect of agency on the perceived temporal relationship between action and its outcome (intentional binding) or perceived intensity of a voluntary action outcome (sensory attenuation) without asking anything about agentic experiences. Therefore, they can be relatively robust against confounding factors and cognitive biases that affect explicit measures and can be successfully used in special populations (Wolpe & Rowe, 2014). However, it should be noted here that implicit and explicit measures might not measure the same target. Although there have been studies showing a relationship between implicit and explicit measures (Berberian, Sarrazin, Le Blaye, & Haggard, 2012; Ebert & Wegner, 2010; Imaizumi & Tanno, 2019; Pyasik, Burin, & Pia, 2018), they might not necessarily be related since they can reflect different constituents of SoA (feeling versus judgement of agency) (Dewey & Knoblich, 2014; Ebert & Wegner, 2010; G Hughes, 2018; Synofzik et al., 2008). In the following section, I will give an overview of the literature regarding these implicit measures that were also used in this thesis as proxies of SoA.

1.3.1 Intentional Binding

Intentional binding refers to the phenomenon that the perceived time of actions and their outcomes shift towards each other (creating a temporal compression of time in between) in comparison to when these events occur alone (Haggard et al., 2002). Intentional binding has been suggested to reflect a process that is linking voluntary actions to their outcomes in time (Haggard et al., 2002; Moore & Obhi, 2012). In this sense, intentional binding is similar to sensorimotor temporal recalibration (section 1.2); however, differently it does not require a delay adaptation process and is considered as an implicit agency measure. Intentional binding has been considered as an implicit measure of SoA since it is specific to voluntary actions and not observed when the action is involuntary (TMS induced action) or passive and it is sensitive to the agency manipulations (Desantis, Roussel, & Waszak, 2011; Engbert, Wohlschläger, & Haggard, 2008; Haggard et al., 2002; however, see: Buehner & Humphreys, 2009).

Figure 1.2 *Libet Clock example. Clock hand completes one full rotation in 2560 ms. Participants are required to report the position of the clock hand at the time of an interest.*

Intentional binding was first shown in a seminal study by Haggard et al. (2002) using Libet Clock method (Libet, Gleason, Wright, & Pearl, 1983). In this method participants were presented with an analogue clock face where they observed a rotating clock hand (Figure 1.2; one rotation was 2.56 second). Participants were required to report the time of an event observing this clock (Figure 1.3). In operant conditions, participants made actions (button press) at a time of their own choosing which resulted in a presentation of an auditory stimulus (outcome, beep sound) that occurred with 250 ms delay. Participants reported the time of either their button presses or beep sounds in different conditions. In baseline conditions, differently from the operant conditions, button presses and beep sounds were not coupled. Hence, participants reported the time of the button press that does not lead to a beep sound or the time of the beep sound that was triggered by the computer at random intervals. By contrasting operant and baseline conditions, Haggard et al. (2002) were able to calculate the perceived temporal shift of actions and auditory stimulus (outcome) towards one another when they were coupled (operant condition) compared to baseline where these events were presented alone (baseline condition). Based on these contrasts they showed the temporal compression between a voluntary action and its outcome.

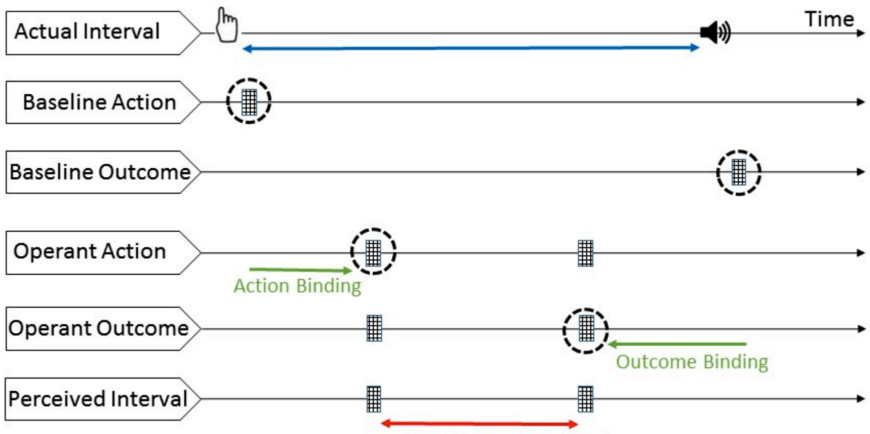

Figure 1.3. *An illustration of intentional binding task. In baseline conditions participants report the time of either their button press or a random beep sound. In operant conditions participants report the time of their action or beep sound but this time these two events are coupled together. That is Button press leads to beep sound and participants report the time of these events in different conditions. Overall intentional binding is the combination of perceived temporal shift of action towards outcome (action binding) and perceived temporal shift of outcome towards action (outcome binding).*

To be able to assess whether this effect was specific to the voluntary actions, Haggard et al. (2002) also had an involuntary action condition in which the action was elicited by transcranial magnetic stimulation (TMS) over the motor cortex (for an alternative method see: Cavazzana, Begliomini, & Bisiacchi, 2014; Engbert et al., 2008). Interestingly, instead of a temporal compression, they found a temporal extension between involuntary action and its outcome suggesting intentional binding was reversed. In another condition included, a sham (placebo) TMS was delivered which was coupled with auditory stimuli. Here, sham TMS does not cause an involuntary action but allowed them to investigate if intentional binding was a consequence of a temporal predictability in the voluntary action condition. They found that sham TMS had the least temporal shift effect (no binding or extension). In the same paper, they presented a second experiment in which they investigated the role of temporal contiguity and temporal predictability on intentional binding effect by manipulating the time interval between voluntary actions and outcomes (250, 450, 650 ms), and predictability of the interval (fixed vs. random). They found that intentional binding was substantially reduced by increased delay between the action and outcome and random intervals suggesting intentional binding process is modulated by temporal contiguity and predictability (factors SoA is also sensitive to). Overall, these findings led them to conclude that voluntary actions and their outcomes can be bound together in time by a special process to create a coherent experience of self-agency.

Action and outcome binding

It is important to note that overall intentional binding effect is a result of a combination of two processes - action and outcome binding. Action binding reflects the temporal shift of the perceived time of the action towards the outcome and outcome binding reflects the temporal shift of the perceived time of outcome towards the action (Figure 1.3) (Haggard et al., 2002). That is perceived time of actions move towards outcome (action binding) and outcomes move towards action (outcome binding) and they create an overall compression of time (overall intentional binding). Action and outcome binding have been shown to be mediated by different mechanisms (Jo, Wittmann, Hinterberger, & Schmidt, 2014; Moore & Haggard, 2008; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010). Disruptions to the pre-supplementary motor area (pre-SMA), an area related to action initiation and outcome prediction (i.e.; efferent copy generation, Haggard & Whitford, 2004), decreased the outcome binding but not action binding suggesting outcome predictions might underlie the outcome binding (Moore et al., 2010). Indeed, the relationship between prediction processes and outcome binding was also supported by the finding that increased early readiness potential, the preparatory cortical activity that precedes the actions and localised to the pre-SMA, was associated with increased outcome bindings but not action binding (Jo et al., 2014). Furthermore, higher level beliefs (believing oneself or other person would be the agent) also influenced only outcome binding but not action binding suggesting the top down modulation of outcome binding but not action binding (Desantis et al., 2011). On the other hand, action binding might be related to both prediction and retrospection (inference based) (Moore & Haggard, 2008) or their integration based on the reliability of the cues (cue integration, discussed further in section 1.4.3) (Wolpe, Haggard, Siebner, & Rowe, 2013).

Intentional binding and SoA

The role of several factors such as intentions, temporal contiguity, causality and predictability in intentional binding is important for understanding this phenomenon's relevance for SoA. In the following section I will give an overview of the research investigating these factors.

The importance of the intentional action was shown in the first study mentioned above (Haggard et al., 2002). In this seminal study, Haggard et al. (2002) found that only intentional actions produce binding effect. That is, the intentional action and its outcome perceived to be closer in time than they actually are whereas unintentional actions (TMS induced motor movement) caused the reverse effect on binding where actions and outcomes got further separated in time. In a later study, Haggard and Clark (2003) investigated whether disruptions to intentions by involuntary movements (TMS induced) would affect intentional binding. They found that intentions that were followed by voluntary actions resulted in binding effect replicating their previous finding. However, intentions followed by involuntary actions did not result in this effect suggesting intentions should match the planned action to create an intentional binding effect. Furthermore, in another experimental design which allowed researchers to investigate the effect of inhibiting intentional actions in the last minute, they found that inhibiting prepared intentional action reversed the binding effect stressing the importance of intentions in binding (Haggard, Poonian, & Walsh, 2009).

In contrast, there have been studies suggesting that intentional action might not be necessary for intentional binding effect and it can be a special case of causal binding (Buehner, 2012; Buehner & Humphreys, 2009). Buehner and Humphreys (2009) found that participants showed greater binding effect when there was a causal relationship between action and the stimulus compared to when there is no causal relationship. Suggesting voluntary action might not be necessary on its own to create binding effect but it might be a special case of a causal binding. In a later study, it was also found that participants showed a binding effect for mechanical causes and voluntary actions once the causality was established; further supporting the idea that causality might be sufficient to elicit a binding effect (Buehner, 2012). However, in these studies relatively longer intervals were used (500 – 1300 ms) which might have downplayed the effect of voluntary action since its effect was shown to decrease with increasing intervals and even absent when it was increased to 650 ms (Haggard et al., 2002). Indeed, in the Experiment 1, for the shortest delay (500 ms) used in the study, voluntary action created more binding effect than the mechanical cause suggesting voluntary action might be creating an additional boost above the causal binding (Buehner, 2012). Since intentional binding reflects the feeling of agency that arises from voluntary action processes, it is possible that it operates in short intervals.

There have been other studies investigating the role of causality and voluntary action and these studies used relatively shorter intervals (200 – 300 ms) compared to Buehner (2012). By factorial manipulation of the causality and voluntary action and asking participants to rate causal relation and measuring intentional binding in separate blocks, Cravo et al. (2009) investigated the role of causality and voluntary action. They found that intentional binding was only found in the conditions where both voluntary action and causal relation was present. This suggested both causal relation and voluntary action is necessary for intentional binding. In another study where they investigated the necessary factors for intentional binding (voluntary action, temporal predictability and temporal contiguity), they found that voluntary actions were necessary for intentional binding effect since temporal predictability between two events did not create a binding effect in the absence of action (Cravo, Claessens, & Baldo, 2011). Furthermore, they showed that temporal predictability and contiguity had impact on binding effect only in voluntary action condition. Overall, these studies, suggest that both voluntary action and causality are necessary factors for intentional binding together with the modulatory effects of temporal predictability and contiguity.

These features of intentional binding such as being dependent on voluntary action and causality as well as being modulated by temporal predictability and contiguity increase its relevance for SoA research.

One prominent aspect of SoA is distinguishing the events that can be attributed to self or others. There have been studies investigating intentional binding effect in situations where the action is performed by the participant or someone else (observed actions) (Engbert et al., 2008, 2007; Haering & Kiesel, 2012; Poonian & Cunnington, 2013; Poonian et al., 2015). Although some studies showed that intentional binding is stronger for voluntary actions compared to observed action conditions (in some cases observed actions did not result in binding as seen in passive action conditions) (Engbert et al., 2008, 2007), there are also studies showing voluntary actions and observed actions create similar levels of intentional binding (Poonian & Cunnington, 2013; Poonian et al., 2015). Studies that found a distinction between self and other’s actions in terms of intentional binding suggested that private information about self-intentions might drive this difference. Studies that found similar levels of intentional binding for self and other’s actions suggested that we might be using similar mechanisms to understand other agents’ actions and the consequences they are causing in the environment. Hence, there is an ambiguity about intentional binding studies on self-agency and other’s agency distinction and it might require further investigation.

In summary, after Haggard et al., (2002)’s seminal study, intentional binding has been replicated in several studies (for reviews: Hughes, Desantis, & Waszak, 2013; Haggard, 2017; Moore & Obhi, 2012; Wolpe & Rowe, 2014), even with different measurement techniques such as interval estimation (reporting the time interval between two events) (Engbert, Wohlschläger, Thomas, & Haggard, 2007; Moore, Wegner, & Haggard, 2009; Poonian, McFadyen, Ogden, & Cunnington, 2015) confirming the effect. As mentioned in this section, intentional binding has been shown to be sensitive to the manipulations that also affect SoA such as causal relationship, voluntary action, temporal predictability and temporal contiguity (Cravo et al., 2009; Cravo, Claessens, & Baldo, 2011; Haggard et al., 2002). Interestingly, believing to be the agent shown to affect intentional binding as well suggesting high level changes in the agency experience can affect intentional binding (Desantis et al., 2011). Therefore, intentional binding has been considered as a reliable implicit measure of SoA (Moore and Obhi, 2012; Moore, 2016) and it was used in this thesis as a proxy of SoA. Since interval estimation type of measures do not allow measuring the two different constituents of overall intentional binding (action and outcome binding), in the empirical studies presented here two mental chronometry methods, Libet Clock and Stream of Letters, were used in the current thesis. This approach allowed to study the effect of development on these constituents of intentional binding (Chapter 3 and 4).

1.3.2 Sensory Attenuation

Another phenomenon that has been associated with SoA is sensory attenuation. Sensory attenuation refers to a decrease in the perceived intensity of a self-generated stimulus (outcome) compared to an externally-generated one (Blakemore, Wolpert, & Frith, 2000; Blakemore et al., 1999; Blakemore, Wolpert, & Frith, 1998). That is, when a stimulus is an outcome of a voluntary action it is perceived as less intense compared to a condition when identical stimulus has an external cause. One famous example of sensory attenuation is that we cannot tickle ourselves. This was investigated by Blakemore et al. (1998) where they showed that when participants controlled a robot arm with one hand to tickle the other hand they experienced reduced perceived ticklishness and intensity in comparison to a condition when the robot arm was controlled by the experimenter. Even though they controlled the robot arm, when temporal distortions were introduced, participants' experience of ticklishness was increased with the increasing delay (0 - 200 ms). Similar findings were also seen with the spatial distortions (Blakemore et al., 1999). Relatively, activation in the somatosensory cortex decreased when the robot hand was controlled by the participants compared to when the robot hand was controlled by the experimenter and this activation was sensitive to the temporal distortions (Blakemore et al., 1998). They suggested that this effect was a result of the outcome predictions (i.e.: efferent copy) regarding the self-generated stimuli so that predicted signal is subtracted from the actual signal causing a cancellation for the self-generated stimulus (see comparator model below in section 1.4.2). However, such processes would not be possible for the externally generated stimuli since internal predictive processes stemming from voluntary actions would not be available due to the stimulus being generated by an external cause. Similarly, sensory attenuation was also observed in auditory (Hughes, Desantis, & Waszak, 2013a; Sato, 2008; Stenner et al., 2014; Weiss, Herwig, & Schütz-Bosbach, 2011) and visual modalities (Cardoso-leite et al., 2010; Hughes & Waszak, 2011).

Sensory attenuation has also been observed as the attenuation of neural responses. It was first reported by Schafer and Marcus (1973) in an EEG study and it has been replicated in several EEG and MEG (Magnetoencephalography) studies since

(Aliu, Houde, & Nagarajan, 2009; Baess, Horváth, Jacobsen, & Schröger, 2011; Baess, Jacobsen, & Schröger, 2008; Cao, Thut, & Gross, 2017; Hughes et al., 2013a). In sensory attenuation studies, typically, an active condition where participants themselves trigger auditory stimuli is compared with a passive condition where a computer triggers auditory stimuli (for reviews: Brown, Adams, Parees, Edwards, & Friston, 2013; Hughes et al., 2013; Waszak et al., 2012). It has been found that N1 auditory event related potential (ERP, first negative peak occurring around 100 ms after the auditory stimulus onset) component to self-generated auditory stimuli was attenuated compared to an externally generated auditory stimuli (Baess et al., 2011, 2008; Hughes et al., 2013a; Schafer & Marcus, 1973). This effect was also observed in MEG counterpart (M100) of N1 and attenuation was localised to the auditory cortex suggesting a modulation of the auditory sensory areas by the motor related processes (Aliu et al., 2009). Although sensory attenuation has been mostly studied by focusing on N1 event related potential (ERP) component, it has been also observed in auditory P2 ERP component, a positive peak around 200 ms following N1 (Behroozmand, Liu, & Larson, 2011; Ford et al., 2001; Knolle, Schröger, Baess, & Kotz, 2012; Sanmiguel, Todd, & Schroger, 2013; Schafer & Marcus, 1973; Sowman, Kuusik, & Johnson, 2012). Furthermore, it has been previously shown via a temporal recalibration paradigm that N1 attenuation did not differ based on the agency judgements (feeling agent or not) whereas P2 attenuation was shown to be higher in conditions where participants judged themselves as the agent compared to the conditions where participants had an illusory lack of agency (Timm, Schönwiesner, Schröger, & SanMiguel, 2016). Furthermore, there was a correlation between P2 attenuation and agency judgements suggesting P2 attenuation might be more related to the agency judgements (Timm et al., 2016). Taken together, sensory attenuation has been suggested to be involved in distinguishing self-generated and externally-generated stimuli since the externally-generated stimulus would be more salient (Blakemore, Wolpert, & Frith, 2002).

1.4 Predictive and Retrospective Components of Sense of Agency

The previous section (1.3) outlined the distinction between judgement and feeling of agency (Synofzik et al., 2008), and introduced two implicit measures of SoA, intentional binding and sensory attenuation. In the current section, I will introduce the main theoretical accounts of how SoA may emerge.

Sense of agency studies mostly come from the two theoretical views that emphasise the external and internal cues in the construction of agency experience. The retrospective view focuses on the retrospective construction of agency experience based on the external cues after an action is executed and the outcome takes place (apparent mental causation) (Ebert & Wegner, 2010; Wegner & Wheatley, 1999). That is inferring agency based on the sensory evidence collected. On the other hand, the predictive view focuses on the internal cues such as intentions, action preparation and prediction of the action-outcome and suggests they play a crucial role on the construction of agency experience (comparator model and pre-activation account) (Frith, Blakemore, & Wolpert, 2000; Haggard et al., 2002; Waszak et al., 2012; Wolpert, Ghahramani, & Jordan, 1995). Later, it was suggested that these external and internal cues arising from the predictive and retrospective processes might be both used depending on their reliability to construct a robust agency experience (cue integration) (Moore & Haggard, 2008; Moore & Fletcher, 2012; Wolpe et al., 2013). In this section, I will introduce apparent mental causation, comparator model, cue-integration and pre-activation account to give an overview of the accounts that have been mainly used to explain how sense of agency may emerge.

1.4.1 Apparent Mental Causation

One strong retrospective account that places stress on the external cues is apparent mental causation. According to apparent mental causation account that was proposed by Wegner and Wheatley (1999), SoA is constructed by inferring causal relationship between the intention and action based on the sensory evidence collected (retrospective explanation of what has happened based on external cues). This approach puts forward three important prerequisites for agency attribution: priority, consistency and exclusivity. That are, intention must be prior to actions, planned action is consistent with actual action and event can only be explained by the one’s action. Based on these, agency is inferred after the event has occurred. This is basically a retrospective sense-making process and if we see our intentions or actions as the most plausible explanation for what just occurred, then we infer self-agency. For example, in an explicit agency study, participants watched themselves in a mirror. However, instead of seeing their own hands they were observing the experimenter’s hands which were positioned in such a way that they look like as if they belonged to the participant. An experimenter performed some actions following the other experimenter’s instructions. When participants could hear these instructions before the actions, they reported enhanced agency over the experimenter’s hands (vicarious agency) whereas this effect was not observed when participants heard the instructions after the action (Wegner, Sparrow, &

Winerman, 2004). Apparent mental causation downsizes the role of voluntary action processes to a great deal. For instance, participants did not necessarily need to perform a voluntary action to feel as an agent in the vicarious agency experiment suggesting internal predictions about the action might not be necessary for agency experience (Wegner et al., 2004).

1.4.2 Comparator Model

The comparator model, on the other hand, emphasizes the key roles of the voluntary action and the motor system in agency experience (Frith, 2005b; Frith et al., 2000; Wolpert & Ghahramani, 2000; Wolpert et al., 1995; Wolpert & Flanagan, 2001). It underlines the importance of internal motor representations of actions and prediction processes that precede the action. According to this model, the motor system executes a chain of processes such as motor command, efferent copy (copy of the motor command that is used for the prediction of the outcome), movement, actual outcome, comparison of predicted and actual outcome and update of predictions (based on the mismatch) to reach a desired goal. According to this account comparison of the predicted and actual outcome is the stage where we establish sense of agency over our actions. That is if the predicted and actual outcome are congruent, agency is attributed to ourselves whereas if there is an incongruence, agency attributed to external sources. Hence, our agency experience depends on the amount of the mismatch (error) between predicted and actual state (for review: David et al., 2008; Frith, 2005b). This account has been mostly used to explain sensory attenuation phenomena, where attenuations accounted by the predictions about the action outcome and the remaining activation represents the mismatch between the predicted and actual state (Blakemore et al., 2000). It should be noted here that this view can be considered as retrospective in nature (Chambon, Sidarus, & Haggard, 2014; Goldberg, Busch, & van der Meer, 2017) because of its proposition about “when” agency is experienced; however, it specifically emphasizes the predictive processes. That is, although the comparison occurs after sensory information about the outcome is available, the nature of the prediction (e.g. experienced agency will depend on the goodness of the prediction from the learned relations between action and the outcome) which is compared to the actual outcome is a vital part of the comparison (Synofzik et al., 2013).

1.4.3 Cue Integration

Recently, these predictive and retrospective approaches have been considered not to contradict but to complement each other. The idea that balanced and context dependent combination of the predictive and retrospective components might be a key factor for a reliable SoA has been suggested (Chambon et al., 2014; Moore & Haggard, 2008; Moore & Fletcher, 2012; Synofzik, Vosgerau, & Lindner, 2009; Synofzik et al., 2013). This is based on the cue integration account which suggests that agency cues (internal and external) are weighted and integrated by taking their reliability into account to construct a dependable SoA. For instance, Moore and Haggard (2008) showed that when the predictability of the outcome is high, when the outcome is predictable enough, intentional binding was observed without any outcome (prediction of an outcome was enough for intentional binding effect); and when the predictability of the outcome was low, when the outcome occurrence was not reliably predictable, intentional binding was observed only when the outcome occurs (outcome was necessary since it cannot be predicted reliably). Based on this study, our brain may be using both predictive and retrospective components to build SoA (also see: Moore et al., 2009) but which process we rely on to construct SoA will depend on the reliability of the predictions. That is the influence of external cue on binding increases with the decreasing reliability of internal cues. This can also be seen in explicit agency experiments, for example, in the vicarious agency experiment described in the above section (1.4.1 apparent mental causation). In that experiment, participants reported self-agency even though it was the experimenter's hand which was doing the actions and participants did not have access to private internal cues such as specific motor predictions. It is possible that absence of internal cues (motor predictions) might have resulted in more weighting on the external cues and participants experienced agency over experimenter's hands this way (Wegner et al., 2004).

In another study, Wolpe et al. (2013) investigated the contribution of cue integration to action and outcome binding separately by manipulating the reliability of the auditory outcome (manipulating the tone intensity). According to cue integration, less reliable cue moves towards the more reliable one. They found that when reliability of the outcome is decreased, perceived temporal shift of action towards outcome (action binding) also decreased but perceived temporal shift of outcome towards action (outcome binding) increased. However, further investigations showed that although cue integration explained the changes in action binding, it could not explain outcome binding (increase in outcome binding was associated with the perceptual shifts in the baseline tone condition when it was not reliable). Wolpe et al. (2013) suggested that the changes they observed in outcome binding might be better explained by pre-activation account (explained in the below section). This was based on the idea that reduced tone intensity against a background noise (increased sensory uncertainty) would lead to increased time for the tone to reach perceptual threshold in the baseline condition; however, when the tone was a consequence of action, the time to reach perceptual threshold would be similar in high and low uncertainty conditions. Hence, this would result in high outcome binding in high uncertainty compared to low uncertainty. Therefore, cue integration contributes to action binding; however, its role for outcome binding is less understood and future studies might be helpful to understand whether cue integration also contributes to outcome binding or it is only a result of a pre-activation mechanism.

1.4.4 Pre-activation Account

Another account that emphasizes the importance of motor prediction was recently suggested by Waszak et al. (2012) to explain how some phenomena that has been used as implicit measures of SoA (intentional binding and sensory attenuation) might occur. Predictive processes that are stemming from voluntary action preparation thought to play a crucial role both in intentional binding (specifically outcome binding) and sensory attenuation by modulating the neural activity in sensory areas through motor prediction (Aliu et al., 2009; Hughes et al., 2013a; Moore et al., 2010; Waszak et al., 2012). Waszak et al., (2012) proposed a common pre-activation account for both outcome binding, perceived temporal shift of outcome towards action, and sensory attenuation. According to this account goal-directed action pre-activates brain areas that are related to the processing of that specific outcome based on the predictions about the outcome. This pre-activation increases the baseline activity which in return reduces the discriminability of the incoming signal compared to a condition where baseline activity is not increased due to no prediction about the signal; consequently, this results in sensory attenuation. Also, increased baseline activity causes predicted outcome signal to reach the detection threshold earlier compared to unpredicted one; consequently, this results in outcome to be perceived earlier (outcome binding). Hence, pre-activation account provides a unifying explanation for how both sensory attenuation and outcome binding may emerge. Both the comparator model and the pre-activation account stress the importance of predictions that are emerging from the voluntary action processes. The main difference is that the comparator model does not propose activations in the areas that are related to the upcoming stimulus (outcome) processing before the stimulus onset as pre-activation does. The role of the predictions in comparator model is to be compared with actual stimulus. Pre-activation account, on the other hand, proposes an activation to some degree as if the stimulus was presented before stimulus presentation. Hence it does not require a comparison.

Supporting evidence for the pre-activation account comes from a study where visual discrimination task was used to measure sensory attenuation (Roussel, Hughes, & Waszak, 2013). Participants learned associations between left and right button press and their consequences respectively. When the corresponding stimulus was congruent with the learned association, participants' contrast discrimination sensitivity was lower compared to when this was incongruent. This suggests predicted visual stimulus lead to difficulty in reaching the perceptual threshold (also see: Roussel, Hughes, & Waszak, 2014). This was suggested to be underlined by a pre-activation mechanism where goal-directed action pre-activates the brain circuits that are related to the processing of that specific stimulus based on the predictions. This pre-activation increases the baseline activity which in return decreases the discriminability of the incoming signal since increased baseline makes incoming signal less salient and less discriminable due to the already ongoing activity in the related areas (Waszak et al., 2012). In another study, after learning associations between left and right button press and face and house stimuli, activations in the fusiform face area (shows selective activation for face) and parahippocampal place area (shows selective activation for places) were observed for actions that were coupled with face or house stimuli respectively even though these stimuli were not presented (Kühn, Seurinck, Fias, & Waszak, 2010). This suggests an activation in the related areas based on the motor prediction about the upcoming stimulus. Furthermore, with a similar design, Hughes and Waszak (2014) showed that the degree of pre-activation was associated with the magnitude of attenuation in an ERP experiment. These studies provide evidence for a pre-activation mechanism for the processing of action outcomes.

In summary, predictive (as discussed in comparator model and pre-activation account) and retrospective components (as discussed in apparent mental causation) seem to play an important role in the construction of agency experience. It is sensible that these processes make contribution based on their reliability for a robust experience of agency as suggested in the cue integration approach. However, how maturational changes in the brain throughout development affect these predictive and retrospective components and their contribution to SoA is not known. Understanding the effects of maturing brain on SoA and contribution of these components to SoA can provide valuable information about the neural mechanisms of SoA as well as providing information for understanding behaviours that are specific to different developmental stages. The present section gave an overall picture of the accounts that tries to explain how SoA may emerge. In the following sections, first, I will give an overview of the brain areas and neural circuits that are involved in SoA (section 1.5) and then I will give an overview of the changes observed in these neural circuits during development, which might give rise to the differences in SoA during the transition from childhood to adulthood (section 1.6).

1.5 Neural Circuits of Sense of Agency – Focus on Implicit Agency

1.5.1 Non-invasive Brain Stimulation Studies

Voluntary action processes and outcome evaluations have been under the spotlight for pinpointing the neural basis of SoA. Non-invasive brain stimulation studies over the last decade have highlighted the involvement of the following regions in implicit agency as measured by intentional binding. These areas include pre-supplementary motor area (Pre-SMA) (Cavazzana, Penolazzi, Begliomini, & Bisiacchi, 2015; Moore et al., 2010), dorsolateral prefrontal cortex (DLPFC) (Khalighinejad, Di Costa, & Haggard, 2016) and angular gyrus (a parietal cortex structure) (Khalighinejad & Haggard, 2015; However, see: Hughes, 2018) that are respectively related to action intention, action selection and outcome monitoring.

One of the first attempts to investigate the brain areas that might be directly involved in the intentional binding process was by Moore et al. (2010) which was done using transcranial magnetic stimulation (TMS). TMS is a non-invasive brain stimulation technique that can temporarily inhibit or excite the area of interest and allows to examine the contribution of this area to the task in hand. They aimed to inhibit neural activity in pre-SMA which is involved in the action preparation processes which also includes outcome prediction (Haggard & Whitford, 2004), and the sensorimotor hand area (SMHA) which is involved in the execution of action and sensorimotor feedback. By comparing these two areas that are thought to potentially contribute to different aspects of intentional binding to an unrelated area (Sensory leg area, S1- Leg area), they attempted to identify the mechanisms that regulate intentional binding. They found that disrupting pre-SMA function decreased intentional binding (less temporal linkage between action and the outcome) especially outcome binding. This finding suggested an involvement of pre-SMA in outcome biding by possibly being involved in the outcome prediction (i.e.: efferent copy generation). On the other hand, disrupting sensorimotor hand area had no significant effect suggesting sensorimotor feedback might have no or less contribution to intentional binding. In summary, results from this study highlight the involvement of the pre-SMA by possibly regulating the predictive processes related to voluntary action (e.g., prediction of the action-outcome) in outcome binding. However, Cavazzana et al. (2015) found that stimulating pre-SMA using transcranial direct current stimulation (tDCS; it sends small electric current to stimulate the area of interest) affected action binding instead of outcome binding. Hence, although pre-SMA seems to be involved in intentional binding, which components of intentional binding is regulated by pre-SMA is not completely clear from brain stimulation studies.

Another tDCS study aimed to investigate contribution of dorsolateral prefrontal cortex (DLPFC) and left parietal cortex (specifically angular gyrus - AG) to intentional binding (Khalighinejad & Haggard, 2015). Previous studies have shown that both the DLPFC and lateral parietal cortex are important for explicit agency judgements (Sperduti, Delaveau, Fossati, & Nadel, 2011). Khalighinejad and Haggard (2015) found that they are also involved in implicit SoA. They found that the left angular gyrus and left DLPFC stimulation decreased intentional binding effect. Specifically, left angular gyrus stimulation decreased outcome binding. However, they found no effect of right angular gyrus stimulation. A later study, however, found that right angular gyrus (no effect of left) stimulation affected agency judgements and, there was no effect of angular gyrus (left and right) stimulation on intentional binding (Hughes, 2018). In a meta-analysis of tDCS studies investigating the involvement of the DLPFC in intentional binding that was conducted by them, Khalighinejad et al. (2016) found that DLPFC stimulation only affected intentional binding when participants were making action selection between alternatives. This suggests stimulation of the DLPFC might affect the action selection aspect of implicit agency.

Overall brain stimulation studies highlighted the involvement of prefrontal and parietal regions that are associated with different aspects of SoA such as action initiation and outcome prediction (pre-SMA, Haggard & Whitford, 2004), action selection and regulation (DLPFC, Khalighinejad et al., 2016; Wood & Grafman, 2003), and outcome monitoring (Angular Gyrus, Farrer et al., 2008).

1.5.2 Neuroimaging Studies

Neuroimaging studies investigating neural basis of SoA (both explicit and implicit) have shown a distributed cortical and subcortical mechanism with a specific stress on the prefrontal, frontal and parietal regions that was studied in the abovementioned brain stimulation studies as well. These areas include dorsolateral prefrontal cortex (DLPFC, action selection) (Fink et al., 1999; Kalighinejad et al., 2016; for review: Sperduti et al., 2011), pre-supplementary motor area (pre-SMA, action planning and initiation) (Miele, Wager, Mitchell, & Metcalfe, 2011; Wolpe et al., 2014), supplementary motor area (SMA, action planning and execution) (Kühn, Brass, & Haggard, 2013), angular gyrus (mismatch monitoring) (Sperduti et al., 2011), hippocampus (associative memory) (Elsner et al., 2002), striatum (action initiation) (Miele et al., 2011) , insula (multisensory integration) (Farrer et al., 2003; Sperduti et al., 2011) and cerebellum (sensory prediction) (Blakemore et al., 1998).

As in brain stimulation studies, pre-SMA/SMA found to be related to both explicit and implicit agency across neuroimaging studies (Elsner et al., 2002; Kühn et al., 2013; Miele et al., 2011; Sperduti et al., 2011; Wolpe et al., 2014). For instance, in an fMRI study, Kühn et al. (2013) found that SMA activation was associated with intentional binding. Furthermore, an ERP study also found an association between pre-SMA and intentional binding (Jo et al., 2014). They found that larger early readiness potential was associated with larger outcome binding scores. Early readiness potential is a negative brain activity starting about 2 seconds prior to the action and localised to the pre-SMA (Shibasaki & Hallett, 2006).

Specifically, studies that has been done with patients in combination with neuroimaging provided valuable information about neural basis and their functional importance for SoA. Wolpe et al. (2014), for example, found that corticobasal syndrome patients (alien limb and apraxia symptoms) show almost four to five times larger intentional binding compared to healthy controls or compared to their unaffected hands. More strikingly, they found that this impaired binding was associated with changes in grey matter volume in pre-SMA and its white matter tracts to prefrontal cortex. This finding is important since it shows that functional connectivity of pre-SMA to prefrontal cortex is vital for the processes of intentional binding; and abnormality of these connections are associated with alien limb and apraxia symptoms which are thought to be closely related to abnormalities in the SoA.

In another fMRI study done with schizophrenia patients, Voss et al. (2017) found that, in healthy participants, angular gyrus activity was negatively related to agency ratings. They also showed a related connectivity between angular gyrus and dorsolateral and rostral prefrontal cortex which is associated with action selection aspect of SoA (Khalighinejad et al., 2016). However, this was not the case for schizophrenia patients. Previous explicit SoA experiments showed angular gyrus activation for mismatches of predicted and actual outcomes suggesting a monitoring role for angular gyrus in SoA process (Farrer et al., 2004; Farrer et al., 2008). Hence, as suggested by Voss et al. (2017), it is possible that information about action selection, which is closely tied to intended outcome, from DLPFC might be sent to angular gyrus for outcome monitoring and mismatch might decrease agency experience as suggested in comparator model (section 1.4.2). However, lack of communication between these areas in schizophrenia patients might be associated with impaired action awareness in schizophrenia. Although angular gyrus (a parietal cortex structure) seems to be involved in explicit agency, its contribution in intentional binding is less clear (Hughes, 2018; Khalighinejad & Haggard, 2015)

In summary, the studies reviewed reveal that, as would be expected, SoA is regulated by a complex network of a number of brain regions that interact with one another. Both non-invasive brain stimulation studies and neuroimaging studies highlight the role of a fronto-parietal network in the regulation of agency experience. Therefore, as suggested in a recent review by Haggard (2017), SoA may emerge from the predictive and retrospective interplays between prefrontal/frontal areas that are involved in action selection, planning and initiation, and parietal regions that are involved in monitoring of these and their outcomes. Critically, this fronto-parietal network undergoes substantial maturational changes from childhood to adulthood, which could result in differences in the agency experience and processes used to construct it (predictive and retrospective components). In the following section, I will give an overview of the maturational changes occurring in these brain areas during the transition from childhood to adulthood with a particular focus on adolescence.

1.6 Development and Sense of Agency

Adolescence starts at puberty and continues until one's mid-twenties (24 years-old) (Sawyer, Azzopardi, Wickremarathne, & Patton, 2018). It has been described as a period of significant changes at the physical, social, emotional and neural levels (Dahl, 2004; Steinberg, 2005). These aspects and possibly their interactions can have effects on the agency experience during adolescence as shown in adult experiments (e.g., emotions and moral decisions affect SoA) (Christensen, Yoshie, Di Costa, & Haggard, 2016; Moretto et al., 2011; Yoshie & Haggard, 2017). In this thesis, I focus on the SoA process during adolescence and its neural correlates since adolescence might be an important period for the development of SoA and could have relevance for understanding the neural correlates of SoA in general, which will be discussed in the following paragraphs. Furthermore, this type of work will provide a basis for the future work that might address other important questions such as effect of peers or emotions on SoA and sense of responsibility over one's actions during adolescence. In this section, I will give an overview of the changes occurring in the brain areas that are important to SoA from childhood to adulthood. I will also introduce developmental studies of SoA (explicit and implicit) which mainly compared children with adults; however, have not examined the adolescence period, which is a focus of my work in Chapter 3 and 4.

1.6.1 Brain Maturation during Adolescence

Brain maturation from childhood to adulthood is characterised by the changes in the white and grey matter (Giedd et al., 1999; Gogtay et al., 2004 Mills et al., 2016). White matter consists of myelinated axons that increase the speed of electrical transmission enabling a fast processing of complex information (Hartline, 2008). Previous studies have found that white matter volume increases linearly across different brain regions during childhood and adolescence continuing into adulthood (Asato, Terwilliger, Woo, & Luna, 2010; Giedd et al., 1999; Mills et al., 2016). These include frontal and parietal regions (Barnea-Goraly et al., 2005; Sowell et al., 1999). For example, a diffusion tensor imaging (DTI) study investigating white matter development in adolescence found that projection fibres connecting prefrontal cortex to striatum and thalamus which contribute to the top down modulations of behaviour continue to mature throughout adolescence (Asato et al., 2010). Increases in white matter with age are suggestive of an increase in structural and functional connectivity which leads to the coherence and synchrony of the neural networks (Hagmann et al., 2010). For instance, a resting state functional connectivity MRI (fcMRI) study found that brain functional maturity was underlined by the declination of the short distance links and increasing long distance functional links that provides associations of distant brain regions and this process continues during adolescence (Dosenbach et al., 2010). The developmental changes in the white matter results in optimizations of cognitive functioning and information processing based on the improving integration of distant brain regions (Ernst, 2014; Nagy, Westerberg, & Klingberg, 2004).

Grey matter, on the other hand, consists of neuronal cell bodies, dendrites and glial cells and it also undergoes maturational changes from childhood to adulthood

(Mills & Tamnes, 2014). In contrast to white matter which increases with age, we see an overall decrease in grey matter where significant reductions in grey matter density was observed in frontal and parietal cortex (Sowell, Thompson, Holmes, Batth, et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell, Thompson, Tessner, & Toga, 2001). For instance, in a longitudinal study, cortical grey matter volume was shown to be highest in childhood and steadily decreased during adolescence and this decrease slowed down during adulthood (Mills et al., 2016). Maturational changes in cortical thickness which represents the area between pia meter/grey matter boundary and grey meter/white matter boundaries (Mills & Tamnes, 2014), has also been investigated. For instance, a longitudinal brain imaging study revealed a decrease in cortical thickness from childhood to adulthood (Zhou, Lebel, Treit, Evans, & Beaulieu, 2015). They observed similar reduction rates during childhood and adulthood in cortical thickness, but increased reduction rates during adolescence. This suggests an accelerated cortical thinning process during adolescence which might represent an important time window of rapid changes in the brain. Another study investigating cortical thickness from the age of 6 to 29 found a linear development in cortical thickness in posterior and superior frontal regions as well as in temporal regions and orbitofrontal areas (Mutlu et al., 2013). On the other hand, there was a quadratic (U-shaped like) developmental trajectory of cortical thickness in the lateral and medial prefrontal regions, and parieto-temporo-occipital junction (also see Ducharme et al., 2016), regions that include SoA related brain areas such as DLPFC and angular gyrus. It should also be noted here that lateral prefrontal regions has reciprocal connections with motor control related areas such as basal ganglia, premotor cortex and supplementary motor area as well as higher order sensory processing related areas such as parietal cortex and association areas (for review: Wood & Grafman, 2003). Hence, developmental changes observed in lateral prefrontal regions can have important influences on motor control and SoA. These linear and quadratic developmental trajectories of cortical thickness in different brain regions represent continuing maturational changes from childhood to adulthood (Mutlu et al., 2013) and accelerated cortical thinning process during adolescence might underline this period as a period of rapid changes in cortical thickness and cognitive abilities (Zhou et al., 2015).

It is interesting that structural and functional connectivity changes occurring from childhood to adulthood do not temporally coincide across different brain regions (Asato et al., 2010; Casey, Getz, & Galvan, 2008; Gogtay et al., 2004; Mills et al., 2016;

Sowell et al., 2003; Sowell et al., 2001); and possibly this temporal inconsistency has high relevance for understanding neural mechanisms of SoA. For instance, Sowell, Thompson, Holmes, Batth, et al. (1999) found that most prominent changes occur in the parietal areas (action-outcome monitoring) from childhood (7-10 years-old) to adolescence (12-16 years-old); and in the frontal regions (dorsal, medial and lateral; action selection, planning and initiation) from adolescence to adulthood (23-30 years-old) (Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). They also showed that prominent maturational changes occur in the striatum from adolescence to adulthood (also see: Barnea-Goraly et al., 2005), an area that can modulate voluntary movements and action initiation (Alexander & Crutcher, 1990). Furthermore, a later study showed an increased reduction of grey matter density in frontal areas and decreased reduction of grey matter density in parietal areas from adolescence to adulthood suggesting maturational changes continuing at higher rates in frontal areas than parietal areas in the transition from adolescence to adulthood (Sowell et al., 2001). In addition, Gogtay et al. (2004) showed that maturation processes start the earliest in the primary sensorimotor areas and the latest in the DLPFC which occur during late-adolescence. These changes that occur at a different pace (at different developmental periods) in different brain regions involved in SoA suggest a possible age-dependent maturational imbalance in the SoA related processes. That is, for instance, mature parietal areas in adolescence and still maturing frontal areas can influence the way predictive and retrospective processes used in the construction of agency experience. Therefore, these maturational changes suggest that there could be key differences in the agency experience from childhood to adulthood and this period might be important for the development of SoA. How individuals compensate for these possible maturational changes during the transition from childhood to adulthood to somehow construct their experiences of agency is an intriguing question, which the work presented in this thesis aims to address.

1.6.2 Sense of Agency in Children and Adults

Although there have been no studies investigating SoA or its neural correlates during adolescence, there were a few studies investigating SoA in children, adults (Cavazzana et al., 2014; Van Elk, Rutjens, & van der Pligt, 2015) and elderly (Cavazzana, Begliomini, & Bisiacchi, 2017; Metcalfe et al., 2010). Focusing on the external judgements of agency, Metcalfe et al. (2010) found that adults (18-24 years-old) were more sensitive to the disturbances over their control compared to both children (8-10 years-old) and elderly participants (mean = 78 years-old). They also showed that children took full credit when their performance was increased artificially suggesting abnormal self-agency attribution over artificial performance increase. In another study investigating explicit judgements of agency in children (7-12 years-old) and young adults (18-25 years-old), Van Elk et al. (2015) found that the judgements of agency got affected by the outcome congruency similarly in children and adults suggesting congruency detection and its effects on judgement of agency starts early on. They also found that children had increased attribution of agency to themselves over positive than negative outcomes, and this effect was stronger for younger children compared to older children suggesting that self-serving bias (i.e. overestimation of self-agency) decreases with maturation. These two studies suggest that there is a developmental effect on explicit judgements of agency and young children are more affected by self-serving bias when judging their agency.

In another study Cavazzana et al. (2014, 2017) used intentional binding to investigate the developmental effects on implicit agency by comparing children (mean age: 10) and adults (mean age: 23). In this study, they used Stream of Letters instead of Libet Clock task suggesting that Libet Clock (a quickly rotating clock hand on a clock face, section 1.3.1) might be difficult for children. Similar to Libet Clock, Stream of Letters is also a mental chronometry task where participants required to watch quickly changing random letters on the screen and report the letter presented at the time of an event of interest. It should be noted here that these two tasks have not been compared previously and they might differ since they have some methodological differences (e.g. predictable clock movement vs. unpredictable letters and temporal precision; Discussed further in Chapter 3). They found that children showed smaller intentional binding compared to adults (discussed further in section 3.1). Considering intentional binding as an implicit SoA measure this finding suggests a decreased SoA in children which contradicts with the above studies suggesting greater SoA (decreased temporal linkage of actions and outcomes) in children compared to adults. Discrepancies between findings explicit and implicit studies can possibly be attributed to the differential nature of the judgement and feeling of agency (Synofzik et al., 2008).

It should be mentioned that explicit and implicit SoA studies mentioned above did not include the adolescence period, which might be necessary to fully understand development of SoA as well as its neural mechanisms. Development can have important effects on correctly attributing agency over self-generated action outcomes since brain areas related to SoA and their connections show protracted development in life as discussed above. Interestingly, these maturational changes (somewhat imbalanced, early maturation in parietal late maturation in frontal areas) might have compensatory influences on the way cognitive processes used to construct agency experience such as relying on retrospective (inference based) or predictive processes more. Hence, as a first attempt to investigate these issues, in the current thesis, I investigate how SoA changes from childhood to adulthood (Chapter 3) and its neural correlates (Chapter 4) from adolescence to adulthood.

1.7 Thesis Outline

This thesis investigated the neural basis of sense of agency by focusing on the perceived action-outcome temporal relations, namely sensorimotor temporal recalibration and intentional binding, using a non-invasive brain stimulation technique (tDCS), developmental approach and EEG.

Chapter 2, in two experiments, investigated the contribution of the sensory specific cortices (auditory and visual) to the sensorimotor temporal recalibration using a non-invasive brain stimulation technique (tDCS). This study also investigated the possible common role of auditory cortex in sensorimotor (in both visual and auditory) temporal recalibration.

In the following chapters (Chapter 3 and 4), I used intentional binding to investigate the neural mechanisms underlying implicit SoA throughout development. I specifically focused on intentional binding since it is an implicit measure of SoA and might better reflect the developmental effects on SoA compared to temporal recalibration which focuses on the adaptation to a temporal delay between two events.

Chapter 3, investigated intentional binding using two different methods (Stream of Letters and Libet Clock) in children (9-10 years-old), mid-adolescents (13-14 years-old), late-adolescents (18-20 years-old) and adults (25-28 years-old). This study also aimed to compare two measurement methods in terms of the intentional binding they measured, developmental trajectory they captured and their suitability in developmental work.

Chapter 4 investigated the neural correlates of the developmental effects found in Chapter 3 by focusing on intentional binding as measured with Libet Clock method in mid-adolescents (13-14 years-old), late-adolescents (18-20 years-old) and adults (25-

28 years old) using EEG. This study specifically designed to investigate ERPs leading up to the action (readiness potential) and ERPs related to self-generated outcome processing (attenuation of auditory evoked potentials such as N1 and P2). Chapter 4 focused on only outcome binding, the perceived temporal shift of outcome towards action, based on the findings from Chapter 3. The main aim of this study was to investigate the neural correlates of the developmental changes in intentional binding by investigating the components that are shown to be associated with the predictive processes in the brain such as readiness potential and sensory attenuation.

Chapter 5, summarizes and discusses the findings from the empirical studies presented in this thesis and suggests future directions that would be informative for understanding mechanisms of SoA and adolescent behaviour.

Chapter 2

2. The role of Auditory and Visual Cortices in Sensorimotor Temporal Recalibration: A tDCS Study

The empirical work presented in this chapter was published as follows: Aytemür, A., Almeida, N., & Lee, K. H. (2017). Differential sensory cortical involvement in auditory and visual sensorimotor temporal recalibration: Evidence from transcranial direct current stimulation (tDCS). Neuropsychologia, 96, 122-128.

Abstract

Adaptation to delayed sensory feedback following action produces a subjective realignment of the time between action and feedback (temporal recalibration effect, TRE). TRE is important for sensory delay compensation to maintain a relationship between causally related events. It is unclear whether TRE is a sensory modality-specific phenomenon. In 2 experiments employing a sensorimotor synchronization task, we investigated this question using cathodal transcranial direct-current stimulation (tDCS). We found that cathodal tDCS over the visual cortex, and to a lesser extent over the auditory cortex, produced decreased visual TRE. However, auditory cortex tDCS did not produce any measurable effects on auditory TRE. Our study revealed different nature of TRE in auditory and visual domains. Visual-motor TRE, which is more variable than auditory TRE, is a sensory modality-specific phenomenon, that might be modulated by the auditory cortex. The robustness of auditory-motor TRE, unaffected by tDCS, suggests the dominance of the auditory system in temporal processing, by providing a frame of reference in the realignment of sensorimotor timing signals.

2.1 Introduction

Temporal recalibration refers to the subjective realignment of asynchronous sensory signals to reduce the timing difference between inter-related stimuli, after adaptation to a constant timing difference between the two stimuli (discussed in section 1.2). For example, when a delayed auditory stimulus (e.g. 150 ms) is repeatedly presented after a visual stimulus, the auditory stimulus is perceived as earlier than the visual stimulus when the delay is subsequently removed (Fujisaki et al., 2004). Temporal recalibration occurs not only between presentation of sensory stimuli, but also between an action and its sensory consequences. For example, Stetson et al. (2006) found that, when participants observed a repeatedly inserted delay between an action and the sensory consequence of that action, this delay adaptation can shift an observer's point of subjective simultaneity (the point where two stimuli are perceived as occurring simultaneously) in the direction of the delay, hence producing a subjective compression of time. Therefore, temporal recalibration is important for sensory delay compensation to maintain a causal relationship between events. However, to date, mechanisms underlying temporal recalibration are not fully understood.

A supramodal mechanism, beyond the modality-specific brain areas regulating sensorimotor temporal recalibration, was proposed by Heron et al. (2009). They found that temporal recalibration can be observed in visual, auditory and tactile modalities, and can be transferred between modalities. For example, using auditory stimulus as an action outcome in the delay adaptation period caused to a temporal recalibration effect in visual modality when using visual stimulus in the testing period and vice versa. Sugano et al. (2010) found consistent results but suggested that temporal recalibration might be an outcome of a shift in the motor component instead of a shift in the sensory component, allowing temporal recalibration transference between modalities. However, some findings are not explained by the supramodal account (Sugano et al., 2012, 2014; Yarrow et al., 2013) or the motor component shift account (Sugano et al., 2012). For instance, using a sensorimotor synchronization task, requiring synchronized finger tapping to a rhythmic sequence of regular stimuli, Sugano et al. (2012) found that temporal recalibration effect (TRE) transfers from visual to auditory modality but not vice versa. One would expect the same transference effect between modalities if there was a supramodal mechanism or shift in the motor component. It is possible that visual timing information is transferred to the auditory system so that visual temporal recalibration can be transferred to auditory modality; however, auditory temporal information may not be transferred to the visual system. This suggests a critical role of the auditory cortex in timing across different stimulus modalities (Grahn, Henry, & Mcauley, 2011; Guttman, Gilroy, & Blake, 2005; Kanai et al., 2011; Meyer, Baumann, Marchina, & Jancke, 2007; Sugano et al., 2012). Therefore, the auditory cortex might be a candidate for amodal time regulation (analogous to visual cortex role in auditory spatial perception, Lewald, Meister, Weidemann, & Töpper, 2004; Zimmer, Lewald, Erb, Grodd, & Karnath, 2004; also see ventriloquism effect, Chen & Vroomen, 2013) and its role might extend to temporal recalibration process. However, this hypothesis has not been tested directly using brain stimulation.

We investigated the critical role of the auditory cortex and visual cortex for temporal recalibration in auditory and visual modalities by using transcranial direct current stimulation (tDCS). tDCS is a non-invasive brain stimulation technique that delivers a small current (typically 1-2mA) through surface electrodes to the scalp, to modulate excitability of neurons underneath the electrodes (Nitsche et al., 2008). We used cathodal tDCS to suppress activity in these sensory cortical areas. Based on previous studies suggesting auditory system dominance in timing processes (Guttman et al., 2005; Kanai et al., 2011; Sugano et al., 2012) we hypothesized that auditory cortex stimulation would significantly impact temporal recalibration regardless of stimulus modality, but visual cortex stimulation would impact visual temporal recalibration only.

We made a start on investigating this issue in a previous experiment we conducted in our laboratory during my master's degree. In this experiment, the procedural details (e.g. stimulus, apparatus, task and tDCS procedures) were same as the experiments reported in this study. We firstly investigated a possibility of double dissociation in a 2 by 2 factorial design to test whether or not temporal recalibration is a sensory modality-specific phenomenon (see Experiment 1 in Aytemür, Almeida, & Lee, 2017). This possibility was not tested before. If temporal recalibration was an entirely sensory specific phenomenon, we would find a cross-over interaction effect: auditory temporal recalibration would only be affected by auditory cortex tDCS, and visual temporal recalibration would only be affected by visual cortex tDCS. Based on auditory cortex dominance in timing, we hypothesized that auditory cortex stimulation would significantly impact temporal recalibration both in auditory and visual modalities.

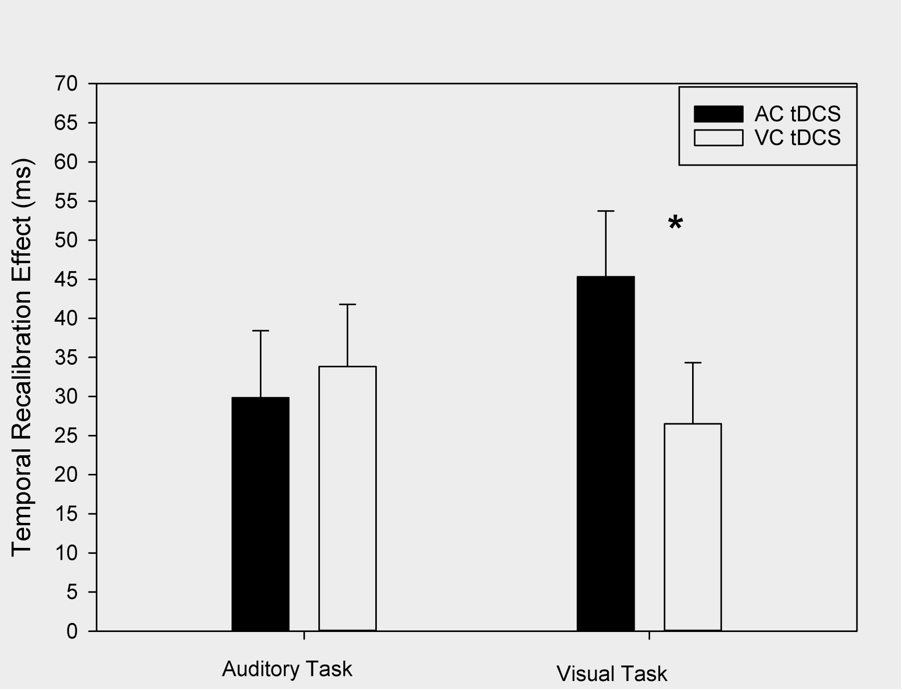

Figure 2.1 *Temporal recalibration effects in auditory cortex (AC) and visual cortex (VC) tDCS conditions in auditory and visual task groups. Errors bars represent SEMs. *p = 0.018.*

We found that, in the visual task, auditory cortex stimulation resulted in higher temporal recalibration effect compared to visual cortex stimulation (Figure 2.1). However, in the auditory task, auditory and visual cortex stimulation did not have differential impacts on TRE. Hence, we did not find the cross-over interaction effect indicating that TRE is a sensory-modality specific phenomenon. However, this experiment did not reveal the involvement of sensory specific brain areas in auditory and visual temporal recalibration since this design did not include a sham condition (placebo). The TRE difference in the visual task could be because of increased visual TRE produced by tDCS over the auditory cortex. Alternatively, it would be consequence of decreased visual TRE as a result of tDCS over the visual cortex. Therefore, in the following two experiments we investigated the involvement of auditory and visual cortices in auditory and visual temporal recalibration by comparing them to a sham stimulation.

2.2 Experiment 1

In Experiment 1, we investigated whether tDCS over the auditory cortex increases or decreases visual TRE. We also aimed to investigate whether auditory cortex stimulation has any effect on auditory temporal recalibration in comparison to a sham stimulation. To do these we employed auditory cortex tDCS and sham tDCS groups in a between-group design.

2.2.1 Method

2.2.1.1 Participants

Sixty student volunteers from the University of Sheffield (20 males, mean age 20.02, SD = 1.39, 4 left handed) were recruited by advertising the experiment in variety of platforms (e.g. classes, friends and university volunteering lists). They had normal or corrected to normal vision and hearing. Participants did not report any history of psychiatric/neurological conditions and seizure disorders. All control variables were reported in Table 2.2. Participants gave informed consent before the experiment. The study was approved by the Department of Psychology Research Ethics Committee at the University of Sheffield.

2.2.1.2 Apparatus and materials

Because timing was of critical importance in this study, we used an open-source Arduino Mega 2560 micro-controller board (ATmega2560) to control experimental events and record data within a few milliseconds timing accuracy (Teikari et al., 2012). Responses were collected using a customized button box (with Sanwa OBSFS 30 Silent arcade buttons) connected to the same Arduino board. The visual stimulus was provided by a small white LED (5mm diameter with a luminance of 4 cd/m^2, attached to the center of a customized 19-inch black background monitor. The duration of the LED stimulus was 10 ms. The auditory stimulus was a binaurally presented tone burst (10 ms duration, 1500 Hz square-wave at a sound pressure level of approximately 74 dB) via Sennheiser HD 202 Stereo headphones. Participants listened to a constant 64 dB white noise to mask the noise of their button presses during the experiment (Sugano et al., 2012). This was done to prevent this noise being perceived as feedbacks.

2.2.1.3 Transcranial Direct-Current Stimulation (tDCS)

Direct current was delivered with two saline-soaked surface sponge electrodes (*cathode electrode:* 5 cm × 5 cm; reference electrode: 5 cm × 7 cm) using a battery-driven constant current regulator (TCT research, Hong Kong). Current strength was 2 mA. We stimulated the right auditory cortex by placing the cathode electrode over T4 according to the international 10-20 EEG electrode placement system. The right auditory cortex was targeted instead of the left, because the right auditory cortex was reported to be involved in both auditory and visual time discrimination tasks in a previous transcranial magnetic stimulation (TMS) study (Kanai et al., 2011).Furthermore, in a previous study it was shown that the right auditory cortex processes stimulus using a long temporal integration window which is within the current time window of investigation (approximately 200 ms), whereas the left auditory cortex process stimulus using short temporal integration window (25-50ms) (Clunies-Ross, Brydges, Nguyen, & Fox, 2015) that is smaller than the time window investigated in this study. In line with these, right sided activity was found in various time perception studies using fMRI (Wiener, Turkeltaub, & Coslett, 2009). Therefore, based on these findings, the right auditory cortex stimulation was chosen to be stimulated in this study instead of the left auditory cortex. The reference electrode was placed over the left cheek over the buccinator muscle, to avoid potential confounding effects of cortical stimulation beneath the reference electrode (Nitsche et al., 2008; Yau, Celnik, Hsiao, & Desmond, 2014). To reduce adverse effects of electric current being delivered abruptly, electric current was increased in a ramp-like fashion over 30 seconds until it reached to 2 mA (Nitsche, Liebetanz, et al., 2003). The stimulation duration of 9 minutes was chosen, because it would produce up to 1-hour aftereffect (Nitsche, Nitsche, et al., 2003) covering the entire duration of our adaptation/post-SMS task sessions (approximately 40 min). For sham tDCS, the current increased in a ramp-like fashion over 30 s and then stopped. This method has been shown to be effective for producing the feeling of the real stimulation to the participants (Gandiga, Hummel, & Cohen, 2006; Yau et al., 2014). During tDCS, some participants reported that they had severe itching (n=1), tingling (n=1), sleepiness (n=2) mood change (n=1) and trouble concentrating (n=2) using the tDCS Adverse Effects Questionnaire (Russowsky Brunoni et al., 2011). These adverse effects did not last beyond the experimental period.

2.2.1.4 Procedure

We used a sensorimotor synchronization task to measure temporal recalibration effect (see Figure 2.4A). In the task, participants are asked to tap in synchrony with a regular sequence of pacing stimuli (auditory or visual). Taps typically precede the stimulus onset by 20 to 80ms on average, which is known as the Negative Mean Asynchrony (NMA) (for reviews: Repp, 2005; Repp & Su, 2013). The NMA is considered to be participant's point of subjective impression of tap-stimulus synchrony (Aschersleben, 2002). Sugano et al. (2012, 2014) have shown that sensorimotor synchronization task can measure temporal recalibration effect by comparing the participants' NMAs before and after delay adaptation. They showed that compared to no-delay adaptation condition, participants who were adapted to 150 ms delay between their button press and feedback had greater NMAs. In our study, using the same paradigm, we applied tDCS over the areas of interest immediately before the delay adaptation period to investigate the effect of stimulating the auditory cortex.

In a between-group design, half of the participants were randomly allocated in the real tDCS condition (N = 30), the remainder half were in the sham tDCS condition (N = 30). All participants performed both auditory and visual tasks in one session before and after tDCS. Task order was counterbalanced across participants, but the same task order before and after tDCS was used for same participant.

In each session, they completed pre-sensorimotor synchronization task just before tDCS and adaptation/post-sensorimotor synchronization task immediately after tDCS. In the pre-sensorimotor synchronization task, they were required to press the button in synchrony with the pacing stimuli. There was a practice trial followed by 25 main trials. In each trial, pacing stimuli (auditory or visual) were presented 15 times with a constant 750 ms inter-stimulus interval. Participants were asked to attend to the first 2 stimuli to get into the rhythm, and then to tap in synchrony with the rest of the stimulus sequence. Immediately after the completion of the pre-sensorimotor synchronization task of 25 trials for each modality (2 x 25 trials in total, no delay adaptation involved), cathodal tDCS over the auditory cortex began for 9 minutes. After the completion of tDCS, participants completed 25 pairs of delay adaptation and post-sensorimotor synchronization trials for each modality (2 x 25 trial pairs). In an adaptation trial, participants voluntarily pressed the button 15 times: they were instructed to keep similar pace to the pre-sensorimotor synchronization task. A feedback stimulus was delivered 150 ms after each button press (i.e., delay adaptation). This delay duration was chosen because it has been shown that approximately 150 ms delay adaptation produced the highest level of temporal recalibration effect (Heron et al., 2009; Stetson et al., 2006). Immediately after one adaptation trial, one post-sensorimotor synchronization task trial began which was identical to the pre-sensorimotor synchronization task. This procedure was shown to successfully elicit temporal recalibration effect previously (Sugano et al., 2012). After completing the task in one modality, participants completed the same task in the other modality with the same order within pre-sensorimotor synchronization and adaptation/post-sensorimotor synchronization tasks. Participants started each trial at a time of their own choosing by pressing the start button. After finishing the experimental tasks, participants completed Goldsmiths Musical Sophistication Index (Müllensiefen, Gingras, Musil, & Stewart, 2014) for controlling possible effects of musical abilities on sensorimotor synchronization task since musical sophistication was shown to be effective on this task (Musicians show better performance than non-musicians; for review: Repp, 2005).

2.2.2 Results

Table 2.1 Means and standard deviations for Negative Mean Asynchronies (NMAs) and Temporal Recalibration Effects (TREs) for two experiments

	Task Modality	Stimulation Area/Type	Pre-test	Post-test	TRE
Experiment 1	Auditory	AC Real	- 111.8 (60.4)	- 131.6 (55.2)	-19.7 (39.4)
		AC Sham	- 125.1 (47.3)	- 147.1 (37.2)	-22.0 (32.9)
	Visual	AC Real	- 90.1 (48.1)	- 106.4 (45.0)	-16.2 (37.4)
		AC Sham	- 74.0 (50.7)	- 108.7 (46.0)	-34.7 (42.1)
Experiment 2		AC Real	- 73.4 (56.3)	- 107.1 (46.4)	-33.7 (42.9)
		VC Real	- 87.6 (55.9)	- 108.3 (50.7)	-20.6 (28.8)
		AC and VC Sham	- 73.6 (52.6)	- 114.5 (50.7)	-40.8 (41.1)

Note: NMAs are presented in millisecond. Negative values indicate tap comes before the stimulus time. Temporal recalibration effect (TRE) calculated as subtracting pre-test performance from post-test performance. Standard deviations are presented in the parenthesis. Variability of the current results are consistent with previous studies using SMS task to measure TR (Sugano et al., 2012; 2014; 2015)

In each trial, negative mean asynchronies (NMAs) above and below two standard deviations were considered as outliers and removed from each trial before obtaining average NMAs across trials for each condition (2.8 % of total data including participants' missing button presses were removed). Temporal recalibration effect (TRE) was calculated by subtracting averaged pre-test NMAs from the averaged post-test NMAs. When the Mauchley sphericity test concerning the homogeneity of variance was violated, we adjusted the degrees of freedom in the following analyses by using the Greenhouse-Geisser correction. Handedness (measured by Edinburgh Handedness Inventory; Oldfield, 1971) and musical sophistication scores (measured by Goldsmiths Musical Sophistication Index; Müllensiefen et al., 2014) were not significantly different between sham and real tDCS groups (p > .05) (See Table 2.2).

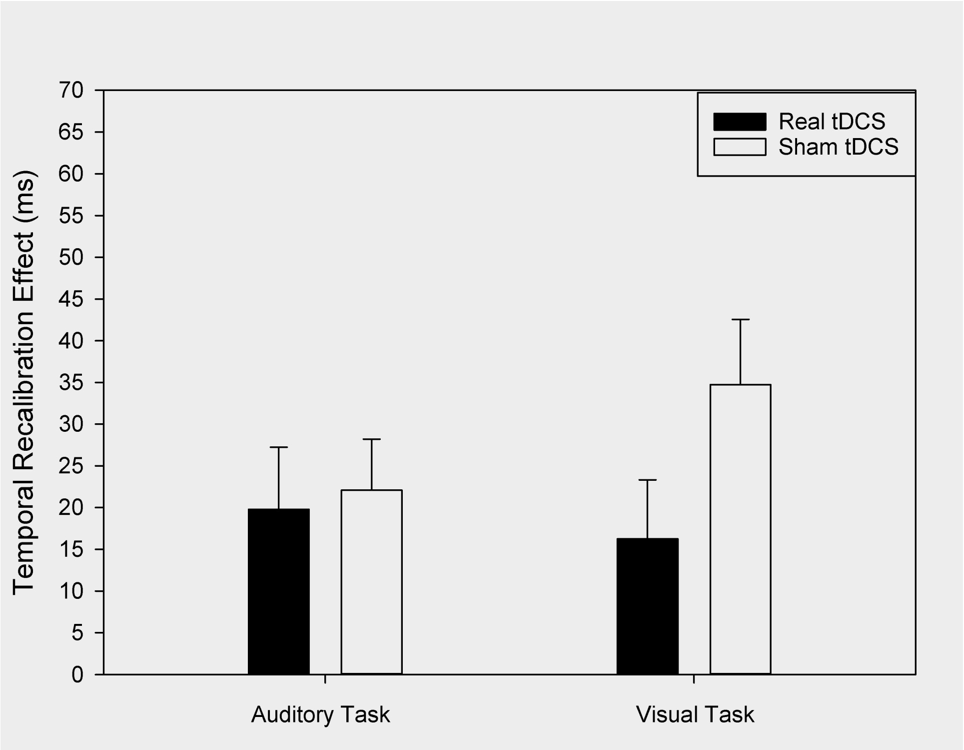

Figure 2.2 *Temporal recalibration effects according to the modality of the task in each stimulation group (auditory cortex real tDCS group vs sham tDCS group). Temporal recalibration effect is calculated by subtracting pre-test negative mean asynchronies from post-test negative mean asynchronies. Error bars represent SEM. Values converted into positive for illustration purposes.*

Three participants were excluded from the further analysis (n = 2 from real, n = 1 from sham tDCS group) due to excessive TRE values (2 SD above group mean). A 2x2 mixed model ANOVA was conducted on TRE values with stimulation group (real vs. sham) as a between-subjects factor and with task modality (auditory vs. visual) as a within-subjects factor. The interaction effect between stimulation condition and task modality was not significant [F (1, 55) = 1.89, p = 0.174, ηp2 = 0.033]. Neither the main effect of group [F (1, 55) = 1.60, p = 0.211, ηp2 = 0.028] nor the main effect of task [F (1, 55) = 0.63, p = 0.441, ηp2 = 0.011] was significant. Nonetheless, as shown in Figure 2.2, we found a trend level of between-group difference in the visual task, which is suggestive of a decreasing visual TRE produced by auditory cortex real tDCS [F (1, 55) = 3.06, p = 0.086, ηp2 = 0.053].

Pre-Test NMA Differences between Groups

Since there were differences in the pre-test NMAs (see Table 2.1), we conducted a 2x2x2 mixed model ANOVA on pre-test NMAs with experimental group (Real vs. Sham AC tDCS) and task order (Auditory vs. Visual Task First) as between-subjects factors and with task modality (Auditory vs. Visual Task) as a within-subjects factor. There was a significant interaction effect between task order and task modality [F (1, 53) = 6.04, p = .017, ηp2 = 0.102]. Pairwise comparisons showed that participants had smaller NMAs when they performed the task again with different modality (auditory task first, F (1, 53) = 4.07, p = 0.049, ηp2 = 0.071; visual task first, F (1, 53) = 29.50, p < 0.001 ηp2 = 0.358). However, task order effect was not significant within each task modality, all ps > .05. This pattern of interaction was supported by a significant main effect of the task modality [F (1, 53) = 27.96, p < .001, ηp2 = 0.345]; participants had larger NMAs in the auditory task than they had in the visual task. There was a significant interaction between experimental group and task modality [F (1, 53) = 4.79, p < .05, ηp2 = 0.083]. Pairwise comparisons showed that participants in Real and Sham stimulation groups did not significantly differ for their pre-test NMAs within each task modality (p > 0.1) suggesting numerical differences we observed in pre-test NMAs did not significantly affected our overall results. Again, this pattern of interaction was supported by the significant main effect of task modality as reported above. There was also no significant main effect of the experimental group on the pre-test NMAs. Finally, neither the main effect of task order [F (1, 53) = 0.034, p = .85] nor its interaction effect with experimental group [F (1, 53) = 1.22, p = .27] was significant.

Table 2.2 Mean control variables age, gender, handedness and musical sophistication for the sub-groups of all three experiments.

	Task Modality	**Stimulation Area/Type**	**Age**	**Gender (number of males)**	**Handedness**	**Musical Sophistication**
Experiment 1	(Auditory /Visual)	AC Real	20.1 (1.7)	10	L: 3.9 (5.2), R: 15.7 (5.3)	60.6 (15.2)
		AC Sham	19.9(1.1)	9	L: 2.1 (3.2), R: 17.9 (3.2)	62.0 (11.0)
Experiment 2	Visual	AC Real	20.9 (5.8)	10	L: 2.9 (4.3), R: 13.7 (5.9)	65.8 (17.7)
		VC Real	19.7 (3.1)	7	L: 5.0 (5.6), R: 11.6 (5.5)	61.8 (11.5)
	Visual	Sham	19.3 (1.3)	6	L: 3.8 (4.3), R: 14.3 (4.5)	61.2 (14.6)

2.3 Experiment 2

In Experiment 1, in a between-group design, we found that auditory TRE was not different between auditory cortex tDCS real and sham groups, consistent with our previous experiment employing a within-group design. Furthermore, an inspection of Figure 2.2 suggested a trend level decrease of visual TRE produced by auditory cortex tDCS. This suggests cathodal tDCS over the auditory cortex might have decreasing effect on visual temporal recalibration. In the previous experiment conducted in our laboratory we found that when participants received cathodal tDCS over the visual cortex, they showed smaller temporal recalibration compared to when they received cathodal tDCS over the auditory cortex (See Figure 2.1, also see Experiment 1 in Aytemür et al., 2017). However, it was unknown if this effect was caused by auditory or visual cortex stimulation. Hence, based on the decreasing effect of cathodal tDCS in the current experiment, the findings from the previous experiment might be caused by the decreasing effect of cathodal tDCS over both auditory and visual cortices. That is cathodal tDCS over both auditory cortex and visual cortex decreased visual temporal recalibration; however, this decrease was more pronounced for the visual cortex stimulation. To directly test this prediction, we performed another experiment comparing the effects of 3 tDCS groups (auditory cortex tDCS, visual cortex tDCS, and sham tDCS) on visual temporal recalibration. We used a between-group design in order to avoid a possible effect of repeated tDCS or task order. We investigated these effects only for visual temporal recalibration because in the previous experiments we did not find any tDCS effects on auditory temporal recalibration process.

2.3.1 Methods

2.3.1.1 Participants, apparatus and materials

Seventy-three student volunteers from the University of Sheffield (25 males, mean age 19.63, sd = 2.48, 12 left-handed) were recruited by advertising the experiment in variety of platforms (e.g. classes, friends and university volunteering lists). As with the previous experiment, all satisfied our inclusion criteria. Apparatus and materials were identical to Experiment 1.

2.3.1.2 Procedure

In a between-group design, approximately one third of the participants were in the auditory cortex real tDCS group (N = 24), the other approximately one third of the participants were in the visual cortex real tDCS group (N = 23) and the remainder of the participants were in the sham tDCS group (N = 26). Participants were allocated to these groups randomly. Half of the participants in the sham group were in the auditory cortex sham group (N = 13) and the remainder half were in the visual cortex sham group (N = 13). For visual cortex stimulation, cathodal electrode was placed over Oz according to international 10-10 electrode placement system. Other specifications of the stimulation procedure were same as Experiment 1. All participants completed visual task which was identical to that used in Experiment 1. The entire experimental procedure lasted approximately 40 minutes including task instructions, practice, tDCS and the main experiment.

2.3.3 Results

Data analysis and outlier removal (3.3% of total data) procedure was the same as for previous experiment. Four participants were excluded from the further analysis (n=3 from VC, n = 1 from sham tDCS group) due to excessive temporal recalibration effects (TREs 2 SD above group means).

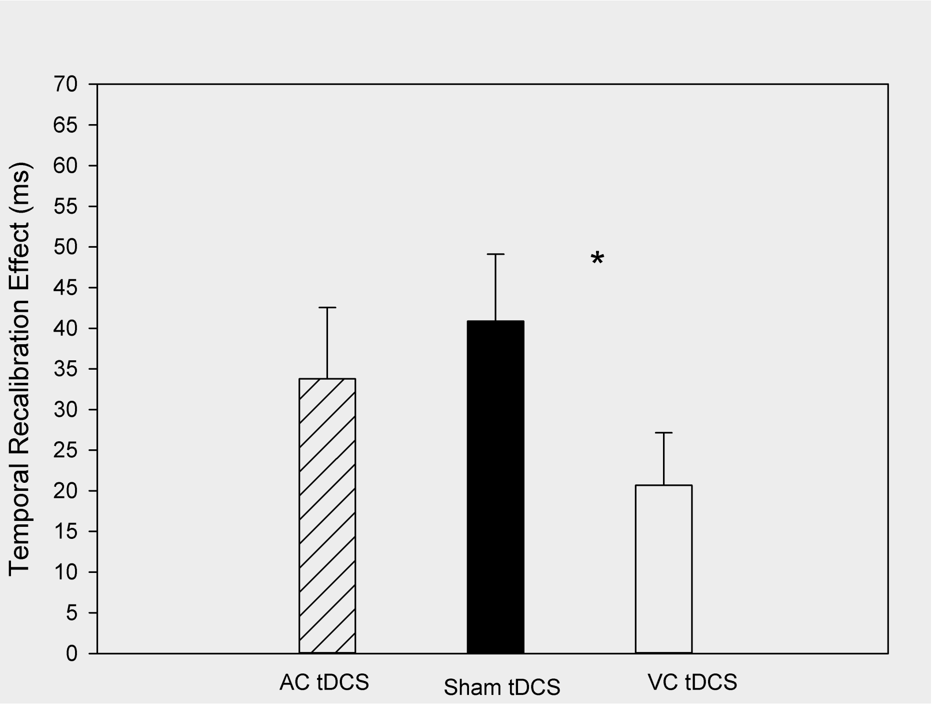

Figure 2.3 *Temporal recalibration effects for the Auditory Cortex (AC), Sham and Visual Cortex (VC) tDCS groups. Temporal recalibration effect is calculated by subtracting pre-test negative mean asynchronies from post-test negative mean asynchronies. Errors bars represent SEMs. Values converted into positive for illustration purposes. *p = 0.035 (one-tailed).*

There was a significant TRE difference between visual cortex real and sham tDCS groups [*t* (43) = -1.856, *p* = .035, d = 0.566, one-tailed]. Therefore, in line with our hypothesis, cathodal visual cortex tDCS had a lowering effect on visual TRE compared to sham tDCS (Figure 2.3). Auditory cortex tDCS group exhibited an intermediate level of TRE that did not differ significantly from either sham tDCS [*t* (42) = 1.160, *p* = .126, one-tailed] or visual tDCS group [*t*(47) = -0.591, *p* = .278, one-tailed].

A one-way ANOVA on pre-test NMAs showed no significant differences between real AC, VC and sham tDCS groups [*F* (2, 66) = .46, *p* > 0.25]. Groups also did not significantly differ for their post-stimulation subjective ratings (in terms of pain, attention and fatigue, *p*s > .25) indicating sham and real tDCS groups had the same perceived tDCS experience. In addition, there was no significant difference between groups in terms of handedness and musical sophistication scores (*p*s > .05).

2.4 Discussion

We investigated the contributions of the auditory and visual cortices to both auditory and visual temporal recalibration effect (TRE). A previously conducted experiment in our laboratory suggested that visual TRE was either affected by auditory cortex tDCS (by increasing TRE) or affected by visual cortex tDCS (by decreasing TRE). In the current study, Experiment 1 showed a trend that auditory cortex tDCS decreased visual TRE compared with sham stimulation. Across these 2 experiments, auditory cortex tDCS did not change auditory TRE. Experiment 2 revealed that visual cortex tDCS significantly decreased visual TRE compared with sham tDCS, but auditory cortex tDCS produced an intermediate effect that did not differ from either visual cortex or sham tDCS effect. Taken together, we found that cathodal tDCS over the visual cortex produced decreased visual TRE. However, both auditory and visual cortex tDCS did not produce any measurable effects on auditory TRE, indicating the robustness of auditory temporal processing.

This study provides direct evidence for the involvement of the visual cortex in visuo-motor temporal recalibration. We found that cathodal tDCS over the visual cortex decreased visual TRE, instead of increasing it. Cathodal tDCS has a neural suppression effect by decreasing neuronal firing rate (Nitsche et al., 2008). Because temporal recalibration is a compensatory process for reducing a temporal delay between causally linked stimuli (Fujisaki et al., 2004), the decrease of TRE following the neural suppression of the primary visual cortex would mean that this compensatory processing is disrupted, and that the mechanism of visual TRE is sensory-specific to the visual system. This explanation is consistent with the perceptual shift account in TRE which suggests the time it takes for the signals to propagate through the brain changes after temporal recalibration (Di Luca, Machulla, & Ernst, 2009; Sugano, Keetels, & Vroomen, 2016a; Yarrow, Minaei, & Arnold, 2015). Our finding suggests perceptual shift of the visual component might have affected by the stimulation (also see Figure 2.4 for more detail). One might argue that visual cortex tDCS slowed down visual sensory processing speed, hence creating a further subjective delay between action and feedback during delay adaptation period. Against this possibility is that the slowing down of processing speed would also affect post-test NMAs. In this case, TRE would be increased rather than decreased. Alternatively, it was possible that visual cortex tDCS did not slow down visual sensory processing speed but that it disrupted an adaptive speeding of the detection of the pacing signal, thus, leading to decreased TRE (see Fig 1 of Sugano et al., 2016).

Our finding that tDCS over visual cortex and to a trend level over auditory cortex produced a decreasing effect of visual TRE is consistent with a previous transcranial magnetic stimulation (TMS) study reporting that both the auditory and visual cortices are involved in visual temporal discrimination process (Kanai et al., 2011). In particular, our finding of auditory cortex involvement during visual temporal recalibration, albeit perhaps weak, suggests that visual TRE can be transferred to the auditory system. This may explain why TRE occurred after adaptation to delayed visual feedback in auditory modality, but not the opposite (Sugano et al., 2012). In line with others, we suggest that temporal information is required to be transformed into auditory representation (Guttman et al., 2005; Kanai et al., 2011; Sugano et al., 2012). If the visual temporal information is being translated into an auditory code, translation might require increased processing load for the visual temporal information than the auditory temporal information. Hence, this process might make visual temporal recalibration more vulnerable to tDCS.

We found that tDCS over the auditory cortex did not produce significant changes in auditory TRE. It has been shown that the auditory system has higher temporal precision and faster processing speed than the visual system (Andreassi & Greco, 1975; Molholm et al., 2002; Stone et al., 2001). Consequently, auditory timing information could be used for a frame of reference for temporal judgements (Di Luca et al., 2009). With tDCS over the auditory cortex, auditory temporal recalibration process would not be affected, because the auditory signal might serve as a reference (i.e., more trusted sensory estimate, see Di Luca et al., 2009 for futher discussion). Hence, we suggest that the perceptual latency shift can occur in the motor component during auditory temporal recalibration, whereas in the visual temporal recalibration this shift can occur in the visual sensory component (Figure 2.4B).

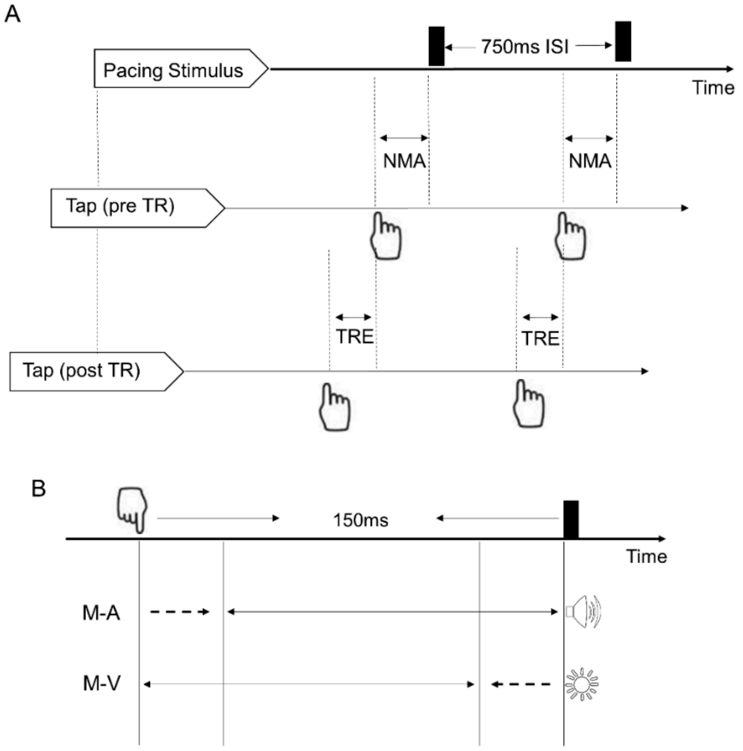

Figure 2.4 *Schematic representation of temporal recalibration in a sensorimotor synchronization paradigm and differential modality effects of delay adaptation. Time is not to scale.* ***(A)*** *A pacing stimulus (either auditory or visual stimulus) was presented 15 times with a constant 750ms inter-stimulus interval. Tapping responses precede the stimulus onset by 20 to 80 milliseconds on average before temporal recalibration (pre-TR tapping). This negative mean asynchrony (NMA) may represent participants' subjective tap-stimulus synchrony. After a delay adaptation phase (illustrated in Figure 4B), participants tap even earlier (post TR tapping) than pre-TR tapping, thereby establishing a new subjective tap-stimulus asynchrony. Temporal recalibration effect (TRE) was obtained by subtracting averaged pre-TR NMA from averaged post TR NMA values. Note that the perceptual element of the pacing stimulus was assumed to be constant (not shifted in post TR) in diagram A.* ***(B)*** *Potential mechanisms of subjective time compression following adaptation to a repeated button press and a delayed feedback. In our study, participants voluntarily pressed the button 15 times and a delayed feedback (150ms) was delivered after each button press. TR produces a subjective time compression between the action and the feedback. Our results suggest that motor-auditory delay adaptation (M-A) causes a slowing down of the motor component (dashed arrow pointing right). This is supported by the robustness of auditory TRE against the effect of tDCS. By contrast, motor-visual delay adaptation (M-V) produces speeding-up of visual processing (dashed arrow pointing left). This is supported by the decreasing effect of visual cortex tDCS on visual TRE.*

Decrease of TRE by applying cathodal tDCS can have therapeutic implications for patients exhibiting increased TRE. Increased TRE can cause an increase of illusory reversals of cause and effect (Stetson et al., 2006) which diminishes sense of agency (SoA: feeling of authorship over one's action). For example, diminished SoA associated with increased TRE (Timm et al., 2014) would result in attributing self-generated thoughts and actions to an external force in schizophrenia. Patients with schizophrenia showed a similar increased contraction of subjective time between their voluntary action and its consequence through an intentional binding paradigm (Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003; Maeda et al., 2012; Voss et al., 2010). Given that visual sensory adaptation could be transferred to auditory TRE (Heron et al., 2009; Sugano et al., 2010, 2012) this transference effect would need to be examined in patient studies when examining auditory TRE for future interventional studies.

2.5 Study Limitations

There are some issues to consider in interpreting our results. First, we found pre-test negative mean asynchrony (NMA) differences between conditions and groups, comparable to those in Sugano et al. (2016), even though handedness and musical sophistication scores, which might affect sensorimotor synchronization task, were not different between groups in our study. NMAs can be affected by several factors such as musical ability, task modality and practice (for review; Repp, 2005; Repp & Su, 2013). The issue of pre-test NMA difference is difficult to resolve. Nonetheless, our control analyses showed that our results were not significantly affected (see the analysis on pre-test NMAs in Experiment 1 and 2). Finally, we chose the right auditory cortex as our stimulation site, based on right auditory cortex involvement in interval discrimination tasks in both auditory and visual modalities (Kanai et al., 2011), and a meta-analytic studies of fMRI time perception studies indicating right-sided auditory cortex activity across various time perception tasks (Wiener et al., 2009). It is possible that we did not stimulate the correct area (i.e., the left auditory cortex) to observe a disruption effect on auditory TRE. Against this possibility was that we observed a modulatory effect (*albeit weak)* of the right auditory cortex on visual TRE. This remote, indirect effect has frequently been reported in both tDCS and TMS literature (Blankenburg et al., 2010; Lang et al., 2005). We suggest that auditory TRE might be difficult to disturb because of the higher temporal precision of the auditory system and faster processing of the auditory modality than the visual modality (Andreassi & Greco, 1975; Molholm et al., 2002; Stone et al., 2001).

2.6 Conclusion

In conclusion, the present study showed, for the first time, that temporal recalibration process can be affected by brain stimulation techniques such as cathodal tDCS. We found robust evidence for modality-specific contribution of the visual cortex on visual temporal recalibration, together with the robustness of auditory temporal recalibration process. Future studies would want to focus on cross-modal temporal recalibration transference and its neural basis, as it may have therapeutic implications for patients with abnormal temporal recalibration and sense of agency. With relatively large samples across two experiments, this study provided a basis for such future studies.

Chapter 3

The studies in Chapter 2 showed the contribution of modality specific brain areas to the sensorimotor temporal recalibration using a brain stimulation technique. Sensorimotor temporal recalibration is considered as a delay adaptation process that brings actions and their delayed outcomes together in time which consequently can influence/facilitate our agency experiences (see section 1.2). In the empirical studies in chapter 3 and chapter 4 we included a developmental approach to be able to investigate the neural basis of sense of agency using a similar phenomenon, intentional binding, that has been used as an implicit measure of sense of agency. We decided to do this since the brain areas that are related to sense of agency go through a maturation process during adolescence, which might result in differences in this experience as well as differences in the neural processes during this period. This could consequently help to understand neural basis of agency experience (see section 1.5 and 1.6). We specifically brought intentional binding on board since it is suggested to be an implicit measure of sense of agency and would reflect the developmental effects on sense of agency.

3. Investigating Implicit Sense of Agency from Childhood to Adulthood using Libet Clock and Stream of Letters

Abstract

Sense of Agency (SoA) is the fundamental feeling that we are in control of our actions and their outcomes. Brain regions associated with SoA undergo significant maturational changes during the transition from childhood to adulthood. This suggests there may be changes in the agency experience throughout development. To investigate this, we examined intentional binding, an implicit measure of SoA, in children (9-10), mid-adolescents (13-14), late-adolescents (18-20) and adults (25-28 years-old). Intentional binding is the perceived temporal attraction between voluntary actions and their outcomes, and it represents the effect of agency on their perceived temporal linkage. Both Libet Clock and Stream of Letters, two measurement methods of intentional binding that has not been examined together before, were used. Using the Libet Clock method, we found a significant age-dependent changes in overall intentional binding which showed a U-shaped trajectory reaching its lowest level in late-adolescence. On the other hand, using the Stream of Letters method, we did not capture significant age-dependent changes in overall intentional binding. In terms of evaluating two tasks; although participants made relatively smaller judgement errors in Stream of Letters, they were less variable in Libet Clock and, consistently, they found Libet Clock to be easier. U-shaped developmental trajectory that reached lowest level in late-adolescence suggest a reduction in the agency experience during late-adolescence since they show a reduced subjective temporal linkage between their actions and outcomes. Considering this temporal attraction as a functional illusion, interestingly late-adolescents might be less affected by it and have more realistic agency experiences whereas younger and older age groups show an over-binding which represents greater agency experiences. This key change in SoA during late-adolescence suggests it is a unique developmental stage in the development of SoA and its underlying processes before adulthood. Further work is needed to understand its functional significance at that developmental stage and why SoA different during late-adolescence compared to earlier or later developmental time-points.

3.1 Introduction

Everyday voluntary actions are accompanied by an intrinsic feeling that we are in control of our actions and their outcomes. Sense of agency (SoA) refers to this fundamental experience, and successful construction of it by the brain is a key element of normal consciousness and mental health (Gallagher, 2000; Haggard, 2017; Pacherie, 2008). The experience of agency is central to everyday voluntary actions (Haggard, 2005, 2017) and impairments in this experience can underline some pathologies such as delusions of control in schizophrenia (Frith et al., 2000; Synofzik et al., 2010; Voss et al., 2010, 2017). SoA is also important for societal and legal systems since it is closely tied to the individuals' responsibility for the outcomes of their actions (Frith, 2014; Haggard & Tsakiris, 2009; Moretto et al., 2011). Adolescence might be an important period for SoA (discussed in Chapter 1) as brain regions associated with SoA (Haggard, 2017; Sperduti et al., 2011) go through a significant maturational process during adolescence (Mills et al., 2016; Sowell, Thompson, Holmes, Jernigan, et al., 1999; Sowell et al., 2001; Zhou et al., 2015). Furthermore, adolescence is associated with a significant vulnerability in developing psychopathologies such as schizophrenia that involve distorted SoA (Gomes, Rincon-Cortes, & Grace, 2017; Harrop & Trower, 2001). However, a developmental approach for understanding possible changes in SoA and their functional implications have been largely neglected. To address this, the current study examined intentional binding, an implicit measure of SoA, in children (9-10), mid-adolescents (13-14) late-adolescents (18-20), and adults (25-28 years-old) using two different measurement methods, Libet Clock and Stream of Letters.

When a voluntary action causes an outcome, they are perceived to shift towards each other in time creating a temporal compression that facilitates the linkage between actions and outcomes. This temporal compression is called intentional binding (Haggard et al., 2002). Intentional binding has been considered as the effect of agency on the perceived action outcome temporal relationship and used as an implicit measure of SoA (Haggard, 2017; Moore & Obhi, 2012) (see section 1.3.1). Overall intentional binding consists of action binding which is perceived temporal shift of action towards outcome and outcome binding which is perceived temporal shift of outcome towards action. These two constituents of intentional binding have been shown to be underlined by different mechanisms such as predictive and retrospective processes. Predictive processes are associated with internal motor processes such as action intention and outcome prediction (i.e., efferent copy) whereas retrospective processes are associated with the external sensory evidence processing and inferring agency retrospectively (section 1.4). Outcome binding was suggested to be underlined by the predictive processes such as outcome prediction whereas action binding was suggested to be underlined by both predictive and retrospective (inference based) processes (Moore & Haggard, 2008b; Wolpe et al., 2013). A combination of action and outcome binding together represents the perceived temporal linkage between actions and their external outcomes.

In adults, intentional binding has been conventionally measured using Libet Clock method (Haggard et al., 2002; Moore & Obhi, 2012). This involves presentation of a quickly rotating clock hand on an analogue clock face (see Figure 3.1B below). Using this method, participants are asked to observe the clock and report the position of the clock hand at the time of an event of interest such as their own button press (action) or beep sound (outcome). In a recent developmental study, an alternative method, Stream of Letters, was used to compare intentional binding between children (mean age:10) and adults (mean age: 23) because Libet Clock might be difficult for children (Cavazzana et al., 2014). In this method, random letters quickly change on the screen and, instead of reporting the clock position, participants similarly report the letter on the screen either when they press the button or hear a beep sound (see Figure 3.1C below). In this study, they found that children show relatively diminished intentional binding compared to adults. This suggests a reduced SoA in children. Cavazzana and collegues' (2014) finding raises a number of interesting questions such as when does implicit SoA becomes adult-like and how it may change throughout adolescence, a developmental period associated with significant final structural and functional brain maturation process (Ernst, 2014; Mills et al., 2016; Nagy et al., 2004; Sowell, Thompson, Holmes, Jernigan, et al., 1999; Zhou et al., 2015).

Adolescence could be an important developmental period for SoA. That is because the brain regions which have been associated with different aspects of agency such as prefrontal/frontal areas that are involved in action selection(dorsolateral prefrontal cortex, DLPFC; Khalighinejad et al., 2016; Wolpe et al., 2014) and action initiation (pre-supplementary motor area, pre-SMA and SMA; Haggard & Whitford, 2004; Moore et al., 2010), and parietal regions that are involved in action and outcome monitoring (angular gyrus; Haggard, 2017; Khalighinejad & Haggard, 2015; Voss et al., 2017) undergoes structural and functional maturational processes from childhood to adulthood (Asato et al., 2010; Casey et al., 2008; Gogtay et al., 2004; Mills et al., 2016; Sowell et al., 2003). Interestingly, these brain regions were reported to go through their final maturational processes at different time periods. For instance, Sowell, Thompson, Holmes, Batth, et al. (1999) found that most prominent changes occur in the parietal regions from childhood (7-10 years-old) to adolescence (12-16 years-old); and in the frontal regions from adolescence (12-16 years-old) to adulthood (23-30 years-old) (Sowell et al., 1999). This suggests large portions of maturational processes occurs before adolescence in parietal regions and during adolescence in frontal regions. They also showed that prominent maturational changes occur in the striatum from adolescence to adulthood (also see Asato et al., 2010), an area that is involved in voluntary movement initiation (Alexander & Crutcher, 1990) and can consequently be involved in SoA. Furthermore, Gogtay et al. (2004) found that DLPFC (associated with action selection) maturation starts in the late-adolescence (also see Mutlu et al., 2013). As these different brain regions mature at different rates age-dependent imbalance in the SoA related process might be evident. For instance, parietal regions responsible for action and outcome monitoring matures from childhood to adolescence but the frontal regions that would feed into this monitoring with action selection, action initiation and outcome prediction processes would still not be fully mature (see section 1.5 and 1.6). Therefore, how individuals construct their experiences of agency throughout development is an intriguing question. However, to date there have been no studies investigating SoA from childhood to adulthood.

To address this, in this study, we used intentional binding as an implicit measure of SoA and we used two different tasks to measure intentional binding, Libet Clock and Stream of Letters. This is because, although Libet Clock and Stream of Letters seem to be similar at first glance, they differ in at least three fundamental ways. First, in Stream of Letters, random letters that are presented on the screen are unpredictable in regard to which letter would occur on the screen next (Cavazzana et al., 2014). In contrast, in the Libet Clock, motion of the clock hand is predictable in regard to where it would move in time (Libet et al., 1983). Quickly changing unpredictable letters might require greater attention which might make the method more difficult especially for children compared to predictably moving clock hand. Also, this contextual predictability versus unpredictability can possibly influence the cognitive strategies used in the task (Moore

& Haggard, 2008; Synofzik et al., 2013). Second, people might find meanings in the letters that are following each other (e.g., NP = no problem, MSC = Master of Science etc.) whereas this would not be the case in Libet Clock. Third, in Stream of Letters, each letter has to stay on the screen for an amount of time (e.g., 150 ms, Cavazzana et al., 2014) that would be of sufficient duration to be perceived by the participant which reduces the method's temporal precision. In Libet Clock the motion of the clock is almost continuous (~42 ms for each clock position, 2560 ms for one rotation, Haggard et al., 2002; Libet et al., 1983). Although Libet Clock provides temporal precision, it might be too fast and might reduce participants' precision when they are reporting the time at which certain events occurred. However, no study to date has examined both methods in the same experiment. By doing so, it would allow us to examine whether any age-dependent differences we observe in SoA would be observed in both tasks, and which one might act as a more reliable method to examine developmental changes in intentional binding.

The present study, investigated the age-dependent changes in SoA from childhood through adolescence into adulthood for the first time, and it used intentional binding as a measure of SoA to benefit from its implicit nature (Haggard, 2017). Considering maturational changes in SoA related brain regions in the transition from childhood to adulthood we predicted a developmental trajectory for intentional binding. What kind of developmental trajectory would be observed during adolescence is of critical importance since we do not know how the maturational changes in different brain regions at different periods would affect the developmental trajectory of intentional binding. Therefore, this trajectory could be observed in different ways as seen in the patterns of behavioural and brain changes during development (linear, adolescent emergent, adolescent specific, Casey, 2015). Cavazzana et al. (2014) suggested that intentional binding is diminished (diminished temporal linkage between voluntary actions and their outcomes) in childhood and it increases towards adulthood. Based on this, it could steadily increase (stronger temporal linkage) from childhood to adulthood (linear), it could increase until a point in adolescence and then be stable (adolescent emergent) or it could increase until a point in adolescence and then decrease back (adolescence specific).

3.2 Methods

3.2.1 Participants

Overall 114 participants were recruited for four different age groups: *children* (N= 21, 11 males, 9-10 years-old, mean age = 9.4, SD = 0.5), *mid-adolescents* (N = 34, 11 males, 13-14 years-old, mean age = 13.35, SD = 0.48), *late-adolescents* (N= 26, 11 males, 18-20 years-old, mean age = 18.9, SD = 0.77) and *adults* (N= 33, 15 males, 25-28 years old, mean age = 26.39, SD = 1.08). These participants were recruited using various methods such as distributing leaflets in coffee shops and libraries and university departments, e-mailing university volunteering lists, contacting schools and advertising the study on social media. Since number of participants recruited without monetary compensation was small (35 participants), we decided to offer £5 for participation (58 participants received monetary compensation). Also, 21 participants received course credits for their participation. Overall, 79 participants were compensated for their time. All participants (and their parents if they were under 18) gave consent before the experiment. Parents were not present in the experiment cubical; however, if they wanted to, they were able to observe the experiment process through a window and were able to enter the cubical. This study was approved by the University of Sheffield, Department of Psychology Ethics Committee.

3.2.2 Materials and Experimental Procedure

For the experimental task, participants sat in front of a computer screen (144 Hz, 24-inch, iiyama ProLite GB2488HSU-B1) in a dimly lit room. PschToolbox 3 (Kleiner et al., 2007) was used to present the two intentional binding tasks. During these tasks participants made button presses using a custom-built button box connected to an Arduino micro-controller (< 2 ms latency; Schubert, D'Ausilio, & Canto, 2013). The auditory stimulus (100 ms duration, 1000 Hz, ~85 dB) was presented using a Sennheiser HD 202 Stereo over-ear headphone.

The same procedure introduced by Haggard et al. (2002) for Libet Clock and Cavazzana et al. (2014) for Stream of Letters tasks were followed. The order of the tasks (Libet Clock First vs. Stream of Letters First) were counterbalanced across participants and the order of the conditions (Baseline Action, Baseline Beep, Experimental Action and Experimental Beep) within each task was randomised. After each task, we asked the youngest (children) and the oldest (adults) age groups to rate the difficulty of the methods on a scale from 1 (very easy) to 7 (very difficult) to be able to assess the perceived difficulty of the measurement methods. This data was only collected from these age groups because the decision to collect such data was made after the interactions with the participants during debriefing (some participants reported finding one task or the other more difficult). Since most of the data was already collected for mid- and late-adolescent groups when this decision was made, we could only collect perceived difficulty reports for children and adult groups.

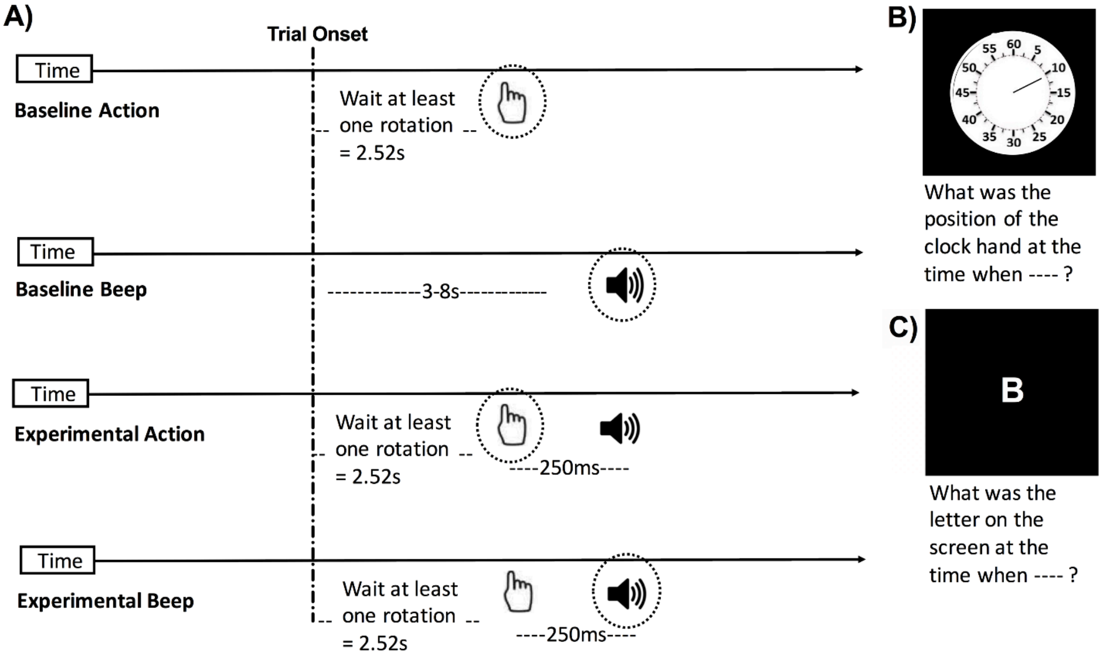

Figure 3.1. **A)** Four conditions in both Libet Clock and Stream of Letters tasks. In *baseline conditions* participants reported the time of either their button press (Baseline Action) or a beep sound (Baseline Beep) that is occurring at a random time between 3 to 8 second after the onset of the trial. Participants started each trial at a time of their own choosing by pressing space button on the keyboard with their left hand. In experimental conditions participants again reported either the time of their button press (Experimental Action) or beep sound (Experimental Beep). However, this time actions were followed by the beep sounds with 250 ms delay. Participants reported the time of the events in dashed circles in relative conditions. **B)** Libet Clock that was used to report the time of the events. Participants were required to report the position of the clock hand at the time of an event of interest. **C)** Stream of Letters that was used to report the time of the events. Participants reported the letter on the screen at the time of an event of interest.

3.2.2.1 Libet Clock task

Libet Clock method involved a clock hand (12 mm) rotating on an analogue clock face (Figure 3.1B). After the start of the trials clock hand appeared at a random position, and started rotating (one rotation: 2520ms). It stopped at a random interval (1.5-2.5s) after the event of interest occurred (button press or beep sound). Clock face was presented on the screen until participants made their reports.

Participants were instructed to observe the Libet Clock and report the position of the clock hand at the time of a button press or a beep sound depending on the condition. There were four conditions *Baseline Action, Baseline Beep, Experimental Action* and *Experimental Beep* in the experiment and each condition consisted of 33 trials. In the *Baseline Action* condition, participants were instructed to make a button press with their right index finger at a time of their own choosing but not before the clock completes one full rotation (Figure 3.1A). They were also asked to make spontaneous button presses instead of reacting to a pre-chosen clock position. The clock hand stopped rotating at a random time between 1.5-2.5s after participants made a button press and disappeared. Participants were asked to report the position of the clock at the time of their button press. In the *Baseline Beep* condition, instead of button press participants were asked to report the position of the clock at the time of a beep sound that was triggered by the computer at a random time between 3-8s after the trial onset. In the *Experimental Action* condition participants made a button press at a time of their own choosing and 250 ms later they heard a beep sound. Then, participants reported the position of the clock at the time when they pressed the button. Similarly, in the Experimental Beep condition, participants pressed the button and after 250 ms they heard a beep sound but this time participants reported the position of the clock at the time of the beep sound.

3.2.2.2 Stream of Letters task

Stream of Letters involved randomly changing letters on the screen (white, capital consonants, 100-point font size) (Figure 3.1C). Random numbers (from 0 to 9) were presented before letters started to appear on the screen for ~2.5s (corresponds to one rotation of the Libet Clock). Each number and letter was presented for 150 ms without any delay in between. Stream of letters stopped at a random interval (1.5 – 2.5s) after the event of interest occurred. Participants were presented with a response map (corresponds to the clock face presented at the end in Libet Clock method) which includes the letter at the time of the event, two letters before and two letters after it. Order of these letters were randomised when they were presented on the screen (Cavazzana et al., 2014).

Participants were instructed to observe the letters and asked to report the letter on the screen at the time of a button press or beep. All the conditions and procedure was same as Libet Clock task. In the conditions when participants were making button presses, they were asked to wait before they make a button press at least until they started to see the randomly changing letters on the screen after the numbers (same as waiting for one rotation in the Libet Clock task).

3.3 Data Analysis

3.3.1 Judgement Errors

First three trials of each condition were considered as practice and were excluded from the data analysis (Cavazzana et al., 2014). Average judgement errors (JEs) were calculated by subtracting the actual time of the event (button press or beep sound) from the reported time of the event in each condition. For all groups, trials with JEs above and below 2SD (Engbert et al., 2007; Wolpe et al., 2013) from the average of each condition were excluded from further analysis for both Libet Clock (Children: 5.1%, Mid-Adolescents: 4.4%, Late-Adolescents: 5% and Adults: 3.8%) and Stream of Letters methods (Children: 2.5%, Mid-Adolescents: 4.5%, Late-Adolescents: 4.1% and Adults: 4.8%). Averages and standard deviations of JEs for each condition were calculated for each task.

3.3.2 Intentional Binding scores

Intentional binding score was calculated as standardly reported in the literature (Haggard et al., 2002). Action binding was calculated by subtracting JE in Baseline Action from Experimental Action condition. Outcome binding was calculated by subtracting the Baseline Beep from Experimental Beep condition. Action and outcome binding represents the perceived temporal shift of action or outcome towards one another respectively in comparison to a baseline. Then, overall intentional binding was calculated as the combination of the magnitude of action and outcome binding which represents the effect of agency on the perceived action-outcome temporal relationship. Judgement error and intentional binding scores for each condition across age groups and tasks can be seen in Table 3.1. Two participants were excluded from the further analysis due to the excessive intentional binding scores in Libet Clock which was more than two times of the delay time (2 X 250 ms) inserted between actions and outcomes and more than 2SD from the group mean (one male participant from mid-adolescent and adult groups with respectively 551 and 589 ms intentional binding scores).

Table 1.1. *Judgement errors and intentional binding scores for Libet Clock (LC) and Stream of Letters (SoL) across age groups and conditions. Negative values represent an anticipatory judgement error. Standard error of means (SEM) presented in brackets.*

		Baseline Action	**Exp. Action**	**Action Binding**	**Baseline Beep**	**Exp. Beep**	**Outcome Binding**	**Overall Binding**
Pre-Adolescent	**LC**	27 (16)	88 (19)	61 (15)	20 (12)	-130 (20)	-150 (18)	211 (22)
	SoL	16 (15)	41 (21)	25 (18)	62 (9)	-79 (17)	-142 (16)	167 (24)
Mid-Adolescent	**LC**	49 (12)	119 (15)	69 (12)	2 (9)	-92 (16)	-94 (14)	163 (17)
	SoL	46 (12)	99 (17)	53 (14)	10 (7)	-57 (13)	-67 (13)	120 (19)
Late-Adolescent	**LC**	47 (14)	94 (17)	47 (14)	-13 (11)	-67 (18)	-54 (16)	101 (19)
	SoL	19 (13)	89 (19)	70 (16)	10 (8)	-88 (15)	-99 (15)	169 (22)
Adult	**LC**	50 (13)	111 (15)	61 (13)	15 (10)	-109 (17)	-124 (15)	185 (17)
	SoL	34 (12)	93 (17)	59 (14)	-4 (8)	-54 (14)	- 50 (13)	109 (20)

3.4 Results

3.4.1 Intentional Binding

3.4.1.1 Developmental Differences in Implicit Sense of Agency

To investigate the developmental trajectory of implicit SoA, a mixed model ANOVA was conducted on the intentional binding scores with Task as a within and Age-Group as a between subject factors. There was a trend level main effect of Task [F (1,108) = 3.48, $p = 0.06$, $\eta p^2 = 0.031$] and its significant interaction with the Age-Group [F (3,108) = 6.09, $p = 0.001$, $\eta p^2 = 0.145$]. Significant developmental differences were found when intentional binding was measured with Libet Clock [F (3,108) = 5.52, $p = 0.01$, $\eta p^2 = 0.133$]. As can be seen in Figure 3.2A, when measured with Libet Clock, intentional binding scores were high in children, and steadily decreased with age until late-adolescence, after which intentional binding increased again to the children level in adulthood. Pairwise comparisons showed that late-adolescents had significantly smaller intentional binding than other age-groups ($p < 0.02$) and mid-adolescents had marginally smaller intentional binding than children ($p = 0.08$). Adults did not significantly differ from children and mid-adolescents ($p > 0.35$). In contrast, no developmental differences were observed when intentional binding was measured with Stream of Letters [F (3,108) = 2.05, $p = 0.110$, $\eta p^2 = 0.054$] (Figure 3.2B).

Following the significant interaction between Task and Age-Group, pairwise comparisons showed that, in children, intentional binding measured with either task did not significantly differ ($p = 0.13$). However, in adults, intentional binding measured with Libet Clock was significantly greater than measured with Stream of Letters task ($p = 0.002$), and this pattern was similar in mid-adolescents, but it was marginally significant ($p = 0.067$). Notably, a different pattern was observed in late-adolescents where intentional binding measured with Stream of Letters was significantly higher than intentional binding measured with Libet Clock ($p = 0.011$).

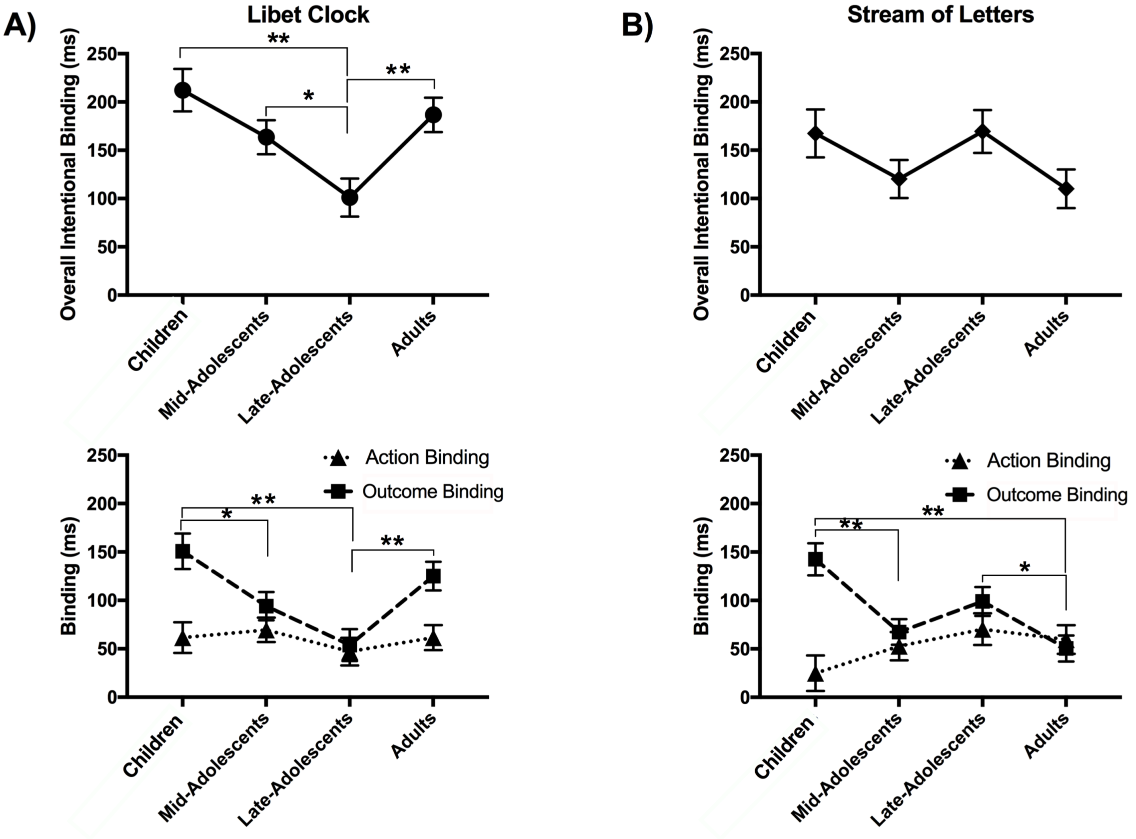

Figure 3.2. *Intentional binding scores measured with the Libet Clock and Stream of Letters tasks. Intentional binding represents the perceived temporal compression between action and its outcome. Action binding is the perceived shift of action towards the outcome and outcome biding is the perceived temporal shift of outcome towards action. Outcome bindings converted into positive scores for illustration purposes.* ***A)*** *Mean overall intentional binding, action binding and outcome binding scores measured by Libet Clock for each age groups.* ***B)*** *Mean overall intentional binding, action binding and outcome binding scores measured by Stream of Letters for each age group.* *$^*p < 0.05$, $^{**}p < 0.005$*

3.4.1.2 Developmental differences in Action and Outcome Binding

We further investigated action and outcome binding's developmental trajectory separately, as they have been suggested to be associated with different processes and might show different developmental trajectories (section 3.1). A mixed model ANOVA was conducted on the binding scores with Task (Libet Clock and Stream of Letters) and Binding Type (Action and Outcome Binding) as within subject, and Age-Groups (Children, Mid-, Late-Adolescents and Adults) as between subject factors. There was a significant Binding Type main effect [$F\,(1,108) = 23.17, p < 0.001, \eta p^2 = 0.177$], two-way Binding Type*Age-Group interaction [$F\,(3,108) = 4.67, p < 0.005, \eta p^2 = 0.115$]

and three-way Binding Type*Age-Group*Task interaction [F (3,108) = 2.82, p = 0.042, ηp^2 = 0.73].

In Libet Clock method, outcome binding, showed the same pattern of changes with age as the overall intentional binding. Outcome binding decreased from childhood to late-adolescence and increased back from late-adolescence to adulthood [F (3,108) = 6.1, p = 0.001, ηp^2 = 0.145] (Figure 3.2A). Pairwise comparisons revealed that children had significantly higher outcome binding both from mid- (p = 0.017) and late-adolescents (p < 0.001) whereas adults' outcome binding did not significantly differ from children (p = 0.28). Late-adolescents had significantly smaller outcome bindings than both adults (p = 0.002) and marginally smaller than mid-adolescents (p = 0.071). In contrast, there were no age-dependent differences in action binding [F (3,108) = 0.46, p = 0.7].

Similar to Libet Clock, in Stream of Letters method, there was also significant Age-Group effect on outcome binding only [F (3,108) = 7.08, p < 0.001, ηp^2 = 0.165] whereas action binding did not significantly change with age [F (3,108) = 1.22, p = 0.3]. As seen in Figure 3.2B, there was an overall decrease of outcome binding from childhood to adulthood with a small increase in the late-adolescence. Pairwise comparisons revealed that children had significantly higher outcome binding than mid-adolescents (p = 0.001) and adults (p < 0.001) and marginally higher outcome binding than late-adolescents (p = 0.054). Adults had significantly smaller outcome binding than late-adolescents (p = 0.017). There was no significant difference between mid- and late-adolescents (p = 0.116). Also, there were no significant difference between mid-adolescents and adults (p = 0.37).

To further investigate whether we observed a binding effect across age groups and task types we conducted another mixed model ANOVA on participants judgement errors with Task (Libet Clock and Stream of Letter) and Condition (Baseline Action, Baseline Beep, Experimental Action and Experimental Beep) as within subject variable and Age-Group as between subject variable. There was a main effect of Condition [F (2.48, 268,56) = 244.50, p < 0.001, ηp^2 = 0.695] and three-way Condition*Task*Age-Group interaction [F (6.72, 242.07) = 2.58, p = 0.015, ηp^2 = 0.067]. Pairwise comparisons showed that there were action and outcome binding effect in all age groups when measured with Libet Clock and Stream of Letters ($p < 0.005$) except that there was not a significant action binding in pre-adolescents when measured with Stream of Letters ($p = 0.176$). That is participants' temporal judgement errors were significantly delayed in Experimental Action conditions compared to Baseline Action conditions and significantly earlier in Experimental Beep conditions than Baseline Beep condition ($p < 0.005$). This result suggests that participants reported the timing of the action later and timing of the outcome earlier in the experimental conditions than the baseline conditions indicating action and outcome binding occurred in the current experiment when both Libet Clock and Stream of Letters methods were used. It should be noted here that pre-adolescent's temporal judgement errors did not significantly differ in Experimental Action condition compared to Baseline Action condition ($p = 0.176$) suggesting action binding did not occur for this group when binding was measured with Stream of Letters method. There were no significant main effect of Task and Age-Group ($p > 0.5$)

3.4.1.3 Relationship between Libet Clock and Stream of Letters

Since Libet Clock and Stream of Letters tasks both measure intentional binding, a high positive correlation would be predicted. To investigate if there is a relationship between the intentional binding measured by Libet Clock and Stream of Letters, we conducted a correlation analysis for overall intentional binding, action binding and outcome binding within each age group. Correlation analysis was conducted between binding measured by Libet Clock and Stream of Letters for each binding type and age group. Since the number of correlations were relatively high, critical p values for significance were corrected using Benjamini-Hochberg correction (Benjamini & Hochberg, 1995). Strikingly, there was not a consistent significant correlation between the binding measured with Libet Clock and Stream of Letters across age-groups (Table 3.2). There was a significant positive correlation only in overall intentional binding in late-adolescents ($r = 0.48$, $p = 0.012$, $N = 26$). These results suggest weak relationship between performances on the two tasks since we did not find a consistent and strong correlation between intentional bindings measured with two tasks. Hence, the assumption that these two tasks are isomorphic must be questioned and considered in future research.

Table 3.2. *Correlation between intentional binding measured by Libet Clock and Stream of Letters in each age group*

	Overall Binding	**Action Binding**	**Outcome Binding**
Children (N = 21)	r = -.08, p = 0.72	r = -.1, p = 0.63	r = 0.45, p = 0.037
Mid-Adolescents (N = 33)	r = .17, p = 0.33	r = .38, p = 0.028	r = -.006, p = 0.97
Late-Adolescents (N =26)	**r = .48, p = 0.012 ***	r = 0.16, p = 0.42	r = -.02, p = 0.92
Adults (N = 32)	r = 0.23, p = 0.2	r = 0.13, p = 0.46	r = .38, p = 0.03

3.4.2 Libet Clock and Stream of Letters

Even though Libet Clock and Stream of Letters methods are methodologically different, they have been suggested to measure the same phenomena (Cavazzana et al., 2014). However, our results showed that they differ in terms of intentional binding they measure and the developmental trajectory they suggest for SoA. Therefore, we further investigated whether these two types of methods would differ from each other with respect to the accuracy of the judgements (judgement error), consistency of the judgements (variability) and perceived difficulty (self-reports).

3.4.2.1 Judgement Errors (JEs)

JEs can be negative or positive since the reported timings can be earlier or later than the real timings. Hence, the magnitude of error quantified by absolute values of JEs were used for this analysis. Absolute JE was calculated for each participant across conditions and tasks. First, Judgement errors made in the Libet Clock and the Stream of Letters tasks were examined in the four age groups tested. A mixed model ANOVA was conducted on the absolute JE scores with Task (Libet Clock and Stream of Letters) and Condition (Baseline-Action, Baseline-Beep, Experimental-Action and Experimental-Beep) as within-subject variables, and Age-Group (Children, Mid-Adolescents, Late-Adolescents, Adults) as a between-subject variable. There was a significant main effect of Task [F (1, 108) = 13.29, $p < 0.001$, $\eta p^2 = 0.11$] where participants showed on average 13.5 ms smaller JEs in Stream of Letters (M = 71, SD = 2.6) compared to Libet

Clock (M = 84.5, SD = 3) method (Figure 3.3A). However, there was no significant interaction of Task with Age-Group or Condition (p > 0.12). There was a significant main effect of Condition [F (1.9, 205.88) = 40.7, $p < 0.001$, $\eta p^2 = 0.274$] and also a condition by Age-Group interaction [F (5.74, 210.49) = 2.64, $p = 0.019$, $\eta p^2 = 0.067$].

Pairwise comparisons showed that all groups had smaller JEs in the baseline conditions compared to experimental conditions. In children, the greatest JE was in Experimental-Beep condition compared to other conditions (p < 0.005) except it did not significantly differ from Experimental-Action condition (p = 1.41) and other conditions did not significantly differ from each other (p > 0.9). In the older age groups, the greatest JE was in Experimental-Action condition compared to other conditions (p < 0.001) except it did not significantly differ from Experimental-Beep condition. Also, older age groups had the smallest JEs in Baseline-Beep condition (p < 0.001) compared to other conditions; however, this was a trend in late-adolescents when compared to Baseline-Action condition (p = 0.08). Furthermore, in Baseline-Action condition, mid-adolescents showed significantly greater JE than late-adolescents (p < 0.05) and there were no other significant differences across age groups in this condition (p > 0.15). In Baseline-Beep condition, children had greater JE than older age-groups (p < 0.005) and other comparisons across age groups were not significant (p > 0.15). In Experimental-Action condition, mid-adolescents had greater JE than children (p = 0.01) and there were no other significant comparisons (p > 0.05). Finally, in Experimental-Beep condition, there were no significant JE differences across age groups (p > 0.05). Overall, participants showed greater JEs in experimental conditions compared to baseline conditions and the age effects on JEs differed based on the condition. There was no main effect of Age-Group ($p = 0.25$).

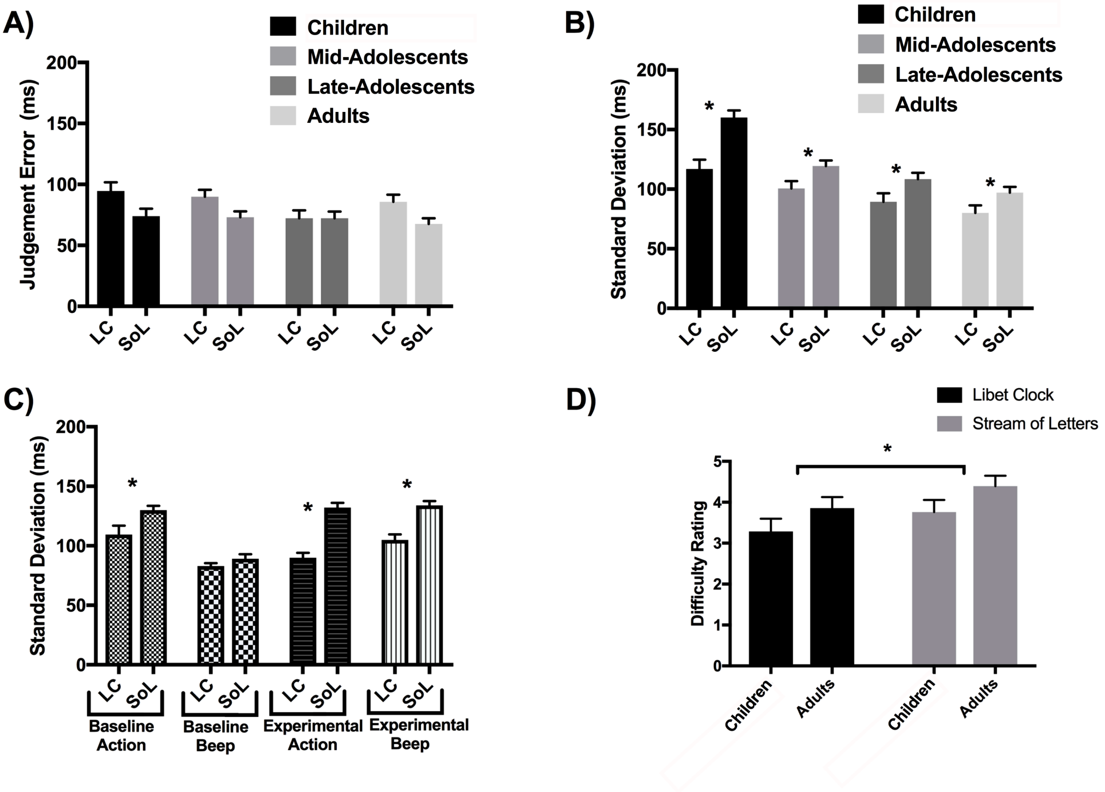

Figure 3.3. ***A)*** *Mean absolute Judgement Errors (JEs) for two tasks across age groups. There was a significant main effect of the task where Stream of Letters (SoL) had on average 13.5 ms lower JE than Libet Clock (LC).* ***B)*** *Mean standard deviations for each task in each age group. There was a significant interaction between task and age group. Less variability was observed in the Libet Clock compared to Stream of Letters across all age groups.* ***C)*** *Mean standard deviations for each task in each condition. There was a significant interaction between task and condition. Variability was smaller for Libet Clock compared to Stream of Letters across conditions except for Baseline-Beep.* ***D)*** *Mean difficulty ratings for each measurement method in pre-adolescents (youngest age group) and adults (oldest age group). There was a main effect of task and age group where Libet Clock was rated as easier than the Stream of Letters and pre-adolescents found the tasks to be easier than adults.* $^*p < 0.05$

3.4.2.2 Variability

Similar to judgement errors, we also analysed the variability of these tasks by calculating the mean standard deviations for each participant across conditions and tasks. As in judgement error analysis, same mixed model ANOVA was conducted but on the average standard deviations this time. There was a significant main effect of the Task [F (1, 108) = 63.71, $p < 0.001$, $\eta p^2 = 0.371$], Age-Group [F (3, 108) = 17.34, $p < 0.001$, $\eta p^2 = 0.325$], and their interaction [F (3, 108) = 2.99, $p = 0.034$, $\eta p^2 = 0.077$]. Pairwise comparisons showed that variability in Libet Clock were significantly smaller compared to variability in Stream of Letters within all Age-Groups ($p < 0.005$, see Figure 3.3B). Furthermore, there were age differences in terms of variability in both tasks. In Libet Clock, children had significantly larger variability than both late-adolescents and adults, and adults had significantly smaller variability than mid-adolescents ($p < 0.05$). Similarly, in Stream of Letters, children had significantly larger variability than the older age groups, and adults had significantly smaller variability than mid-adolescents ($p < 0.005$). There were no significant differences between other comparisons ($p > 0.05$). Furthermore, there was a significant main effect of Condition [F (2.75, 297.86) = 31.97, $p < 0.001$, $\eta p^2 = 0.228$] and its interaction with Task [F (2.82, 304.52) = 9.83, $p < 0.001$, $\eta p^2 = 0.083$]. Pairwise comparisons showed that Libet Clock had significantly lower variability compared to Stream of Letters in all conditions ($p < 0.005$) apart from the Baseline-Beep condition ($p = 0.15$), and the smallest variability both in Libet Clock and Stream of letters tasks was observed in Baseline Beep condition (Figure 3.3C).

3.4.2.3 Self-reports of task difficulty

We also investigated the perceived difficulty of Libet Clock and Stream of Letters by investigating participants' self-reports on a scale from 1 (very easy) to 7 (very difficult) for each task. This data was collected from children and adults (see section 3.2.2 materials and experimental procedure). A mixed model ANOVA was conducted with Task (Libet Clock and Stream of Letters) as a within subject factor and Age-Group as a between subject factor. There was a main effect of the Task where Libet Clock reported to be easier than Stream of Letters [F (1, 46) = 5.46, $p = 0.024$, $\eta p^2 = 0.106$] (Figure 3.3D). There was also significant main effect of Age-Group suggesting children reported that they found the tasks to be easier in comparison to adults [F (1, 47) = 5.22, $p = 0.027$, $\eta p^2 = 0.102$]. This is interesting, as their JE variability scores, which were higher in both tasks compared to adults, would suggest they found the tasks more difficult. There was no interaction between Task and Age-Group ($p = 0.89$).

3.5 Discussion

This study investigated the developmental trajectory of SoA as indexed by intentional binding from childhood to adulthood using Libet Clock and Stream of Letters tasks. As predicted a significant developmental effect was found on intentional binding as measured by Libet Clock, where it decreased from childhood to late-adolescence and increased back to childhood levels in adulthood. This decrease in intentional binding was observed in mid-adolescence first and reached its lowest levels in late-adolescence suggesting an adolescence-specific effect on implicit SoA starting in mid-adolescence and reaching its maximum during-late adolescence. In contrast, no age group differences were observed in intentional binding as measured by Stream of Letters task. Interestingly, separate follow on analysis of action and outcome binding revealed developmental effects on outcome binding but not action binding as measured by both methods suggesting an earlier development for action binding but a prolonged developmental effect for outcome binding. In addition, notably, intentional binding scores in two tasks did not have a consistent and strong correlation across age groups suggesting they might be measuring different aspects of intentional binding. Furthermore, we found that participants' timing judgement errors were smaller on average in Stream of Letters but their judgements were less variable in Libet Clock. Consistent with participants' variability in judgement errors, children and adults reported that they found performing the Libet Clock to be easier than Stream of Letters.

Developmental trajectory of intentional binding and its relationship to brain maturation and cognitive processes

Our finding that intentional binding as measured with the Libet Clock decreases from childhood to late-adolescence and increases back in the adulthood (to childhood levels) suggests an adolescent-specific developmental effect on SoA with an exaggerated agency experience in children and adults. Adolescence is a critical developmental period where the brain undergoes a substantial remodelling process specifically underlined by final maturational changes in the frontal areas together with grey matter decrease and white matter increase which improves the efficiency and the connectivity of the system (Asato et al., 2010; Luna et al., 2001; Sowell et al., 2003, 1999). The maturation and improving connectivity of the brain areas including SoA related ones such as pre-frontal/ frontal (DLPFC and pre-SMA/ SMA), striatum and parietal (angular gyrus) regions until late-adolescence (section 1.6.1) might consequently be reflected in reduced temporal linkage between actions and outcomes in late-adolescence. This might result in more realistic action outcome temporal relationship in comparison to children. That is because late-adolescents show smaller intentional binding effect reflecting that the perceived temporal gap between action and outcome is closer to the temporal gap introduced between action and the outcome in the experiment (250ms, see section 3.2). This suggests late-adolescents might have a more realistic perception of action outcome temporal linkage. However, one would expect this gain to stabilise from late-adolescence to adulthood or continue to improve until adulthood with similar or even less intentional binding in adults. However, this was not the case, intentional binding in adults increased back approximately to the children's level. Therefore, heightened SoA reflected by intentional binding in adults is difficult to reconcile with this brain maturation view at first glance.

One possible explanation for the developmental rebound effect observed in adults might be related to the shifts in cognitive strategies used when constructing the agency experience with age differences in brain maturity. It has been previously suggested that a balanced and context dependent combination of retrospective and predictive processes would be necessary for constructing a reliable SoA (Chambon et al., 2014; Haggard, 2017; Moore & Fletcher, 2012; Synofzik et al., 2013). Retrospective processes are underlined by external cues that takes place after action and outcome occurrence, and involved in inferring causal relationship between intentions and actions retrospectively based on the sensory evidence collected (retrospective explanation of what has happened based on external cues) (Chambon et al., 2014; Haggard, 2017; Wegner, 2002; Wegner & Wheatley, 1999). On the other hand, predictive processes result from internal cues that takes place before the action is performed such as intentions, action preparation and predicting outcomes and involved in the construction of agency experience prospectively (Chambon et al., 2014; Waszak et al., 2012; Yoshie & Haggard, 2017). Moore & Haggard, (2008) previously showed that when the outcome occurrence is highly predictable, intentional binding, specifically action binding, was observed without any outcome (prediction of an outcome was enough for intentional binding effect); and when the predictability of the outcome is low, action binding was observed only when outcome occurs (outcome was necessary since it cannot be predicted reliably). According to this, we may be using both predictive and retrospective processes to build experience of agency but which one to be used might depend on the reliability of the predictions.

In line with this, the developmental change in intentional binding that we found in this study might reflect a developmental shift from relying on retrospective to predictive processes developmentally from childhood to adulthood with a balance between in the engagement of these two processes occurring in the late-adolescence. It is possible that we observed retrospective over-binding in childhood and predictive over-binding in adulthood but a balanced combination of these in late-adolescence (see Figure 3.4). Hence, children might have based their SoA on retrospective processes; in other words, they "explained away" what just happened based on the sensory evidence collected since their predictive processes might not be reliable due to the late maturation of the related brain areas and/or their functional connectivity (fronto-parietal network). On the other hand, adults may have based their SoA on predictive processes; in other words, they "predicted away" what is going to happen based on the strong learned priors about the action outcomes. Hence, both scenarios caused high intentional binding associated with exaggerated agency. In contrast, late-adolescents might have based their SoA on a balanced combination of predictive and retrospective processes which can help them to have an experience of agency that is closer to the reality. If this is the case, this whole process can basically be considered as a developmental transition from using external cues to internal cues when constructing the experience of agency from childhood to adulthood based on the reliability of the predictions. The balance between these processes during the late-adolescence might be beneficial to refine the predictive processes and reduce the errors that might occur in adulthood. It should be noted here that this developmental shift started to be seen in mid-adolescents. This hypothesis needs to be tested in the future studies possibly using a similar experimental design to (Moore & Haggard, 2008) where they manipulated the probability of the outcome occurrence or using EEG to isolate these processes (e.g. recording the readiness potential or auditory N1 attenuation to investigate the predictive processes).

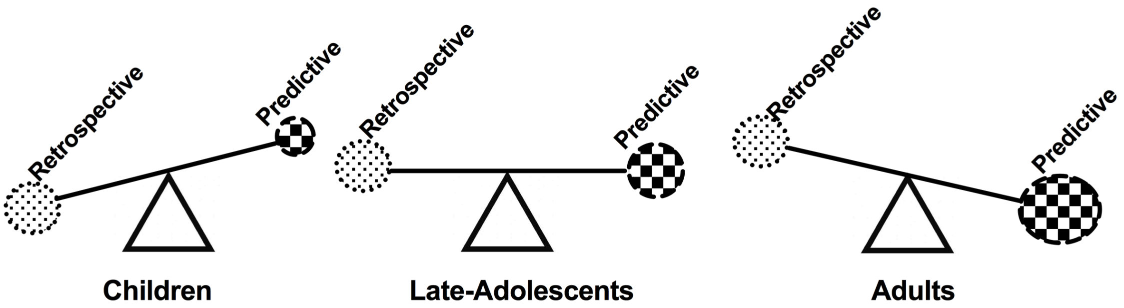

Figure 3.4 *An illustration of the developmental shift that might be observed in the balance of retrospective and predictive processes when constructing SoA experience. Children might be using retrospective processes more (explaining away) since underlying neural mechanism such as parietal regions mature earlier whereas predictive processes are not reliable due to later maturation of the underlying areas (DLPFC and Pre-SMA). With the maturation of the frontal areas that are related to the predictive processes in SoA (DLPFC and Pre-SMA) and consequently increased reliability, adults might be using predictive processes more which might be more advantageous in predictable situations (predicting away). A balance between retrospective and predictive processes might be reached during late-adolescence which results in a performance that is closer to the reality in terms of intentional binding.*

Interestingly, the developmental trajectory we observed in overall intentional binding seems to be underlined by outcome binding, but not action binding. We found that outcome binding followed the same developmental trajectory with overall intentional binding. In contrast, there were no changes in action binding in the transition from childhood to adulthood suggesting an earlier maturation for the processes underlying action binding. This differential developmental trajectory for action and outcome binding was observed using both measurement methods. Albeit, outcome binding showed somewhat different trajectory across measurement methods suggesting it was task-dependent. The main difference was in adult group, there was an increase of outcome binding when measured with Libet Clock whereas there was a decrease of outcome binding when measured with Stream of Letters from late-adolescence to adulthood. This difference might be related to the predictable versus unpredictable nature of the Libet Clock and Stream of Letters respectively. Predictable clock hand movement in the Libet Clock might have increased the use of predictive processes since participants would be able to predict the position of the clock at the time of the outcome occurrence. That is, for instance, participants perceiving the time between action and the outcome shorter would predict the outcome to occur earlier and report its occurrence as earlier as predicted on the clock. However, this would not be the case in Stream of Letters task since quickly changing random letters would not allow to predict which letter would be on the screen at the time of the outcome occurrence and they would need to retrospectively judge which letter was on screen instead of predicting which letter would be on the screen (they cannot know the letter beforehand). Consequently, this can result in low predictive binding in adulthood.

Differential effects of age on action and outcome binding suggest that the mechanisms regulating these processes might have different developmental trajectory. For instance, action and outcome binding have been suggested to be mediated by different mechanisms previously. That is outcome binding is more associated with predictive processes (Waszak et al., 2012) whereas action binding is associated with both retrospective and predictive processes (Moore & Haggard, 2008). It is possible that prolonged changes occurring in the outcome binding reflects a prolonged maturation in the predictive processes. It is also possible that the lack of age effect on action binding might reflect earlier maturation of retrospective processes. However, it should be noted here that involvement of retrospective processes in outcome binding has not been investigated as it was done in action binding (Moore and Haggard, 2008) and should be examined in the future studies. Nevertheless, predictive processes involvement in outcome binding was also suggested by neuroimaging studies. For instance, it was found that disruptions to the pre-SMA, an area related to action initiation and generating efferent copy, diminished outcome binding but not action binding in adults (Moore et al., 2010). In line with this, in another study, early readiness potential, motor related cortical activity prior to actions that is localised to pre-SMA, was associated with outcome binding but not action binding (Jo et al., 2014). It was also found that stimulating angular gyrus, an area related to action and outcome monitoring, affected only outcome binding (Khalighinejad & Haggard, 2015). Taken together, the prolonged developmental changes we observed in outcome binding might be related to the slow maturational changes in the predictive processes underlined by the fronto-parietal network that is regulating it but developmental changes in action binding which probably occurs before adolescence remains less clear.

What would be the implications of developmental changes observed in implicit SoA indexed by intentional binding from childhood to adulthood? Intentional binding might be considered as a temporal illusion that might facilitate or be facilitated by SoA.

This illusion could be functional for experiencing control over our everyday voluntary actions. Increased illusion during childhood and adulthood might be motivational since they would feel in charge of what they do. This might be especially beneficial for children in terms of having facilitatory effect on learning action-outcome relations. However, it should be considered that, experiencing exaggerated control on also negative outcomes might cause problems in children (e.g. feeling mistakenly responsible for a close one dying); albeit, it is worth to note that children might be showing selective increased agency over positive outcomes than negative (Van Elk et al., 2015) which might be protective against this. By contrast, our findings suggest that mid- and late-adolescents might be experiencing less implicit control over their actions. The implications of this need further study. One could posit that this might have negative consequences during adolescence, a period associated with increased distress (Casey, 2015; Steinberg, 2005). A reduction in implicit SoA may facilitate an increase in vulnerability to experience mental health and behavioural problems such as depression, mood disorders and substance abuse during this period since they might feel less control over what they do in daily life ('burden of reality'). On the other hand, successfully handling of this realistic experience might help late-adolescents to master the cognitive strategies being used for agency attribution (predictive vs. retrospective) based on the contextual requirements (low vs high predictable contexts) in adulthood. That is, they might learn to rely on predictive processes when constructing their agency experience in reliably predictable contexts and to rely on retrospective processes (inference based) when the predictive processes are less reliable.

Developmental trajectory of implicit agency is consistent with explicit studies

Our finding that children show an increased SoA associated with increased intentional binding is consistent with other studies focusing on the metacognition of agency. They found that children show increased SoA especially for the artificial performance increase (Metcalfe et al., 2010) and positive action outcomes (Van Elk et al., 2015) suggesting an increased self-agency bias in children compared to adults. It should be noted here that their adult group (M = 20 years-old in Van Elk et al. (2015) and between 18-24 years old in Metcalfe et al. (2010)) corresponds approximately to our late-adolescent age group (age range: 18-20). Hence, our decreasing intentional binding up to late-adolescence is in line with decreased judgement of agency observed in these studies. However, our findings do not support another intentional binding study which used Stream of Letters (Cavazzana et al., 2014). They found that children show a relatively diminished intentional binding effect mediated by a reduction in action binding compared to adults suggesting a reduced SoA for children. In contrast, we found a lack of age effect on overall intentional binding when measured by Stream of Letters. Considering action and outcome binding separately, we found a significant age effect on outcome binding but not action binding. Although we followed similar Stream of Letters procedure as used by Cavazzana et al., (2014), there was a main difference between Cavazzana et al., (2014) and the study presented here. Differently from this study they included passive action conditions where a machine was pressing participants' fingers to make the button press action. It is possible that this condition might have increased children's awareness about the fact that they might not be the agent all the time in general whereas adults were not influenced by this contextual effect. Although this might facilitate the differential findings, further investigations might be useful to understand the nature of this possible effect.

Differential nature of Libet Clock and Stream of Letters methods

Our comparisons between Libet Clock and Stream of Letters revealed that although participants were on average approximately 14 ms closer to the real timings of the events when using Stream of Letters, participants showed less variability in their judgements when performing with the Libet Clock in all age groups and conditions (except for the baseline beep condition where they did not significantly differ). Furthermore, children's and adults' ratings on the difficulty of the tasks showed that they found Libet Clock to be easier than Stream of Letters method. These findings suggest that although Stream of Letters might result in closer judgements to real timings of the events on average, Libet Clock might be easier and more stable when judging the time of the events in all age groups and in most of the conditions. Smaller variability would be more beneficial in intentional binding tasks than smaller judgement errors. This is because baseline correction (subtracting judgement errors in baseline conditions from experimental conditions) in intentional binding tasks would eliminate the judgement error differences in terms of measuring intentional binding effect but higher variability of the measurement would not be compensated. Therefore, Libet Clock, which seems to be more stable measure with less variability, would be beneficial in terms of measuring intentional binding and capturing the experimental effects. Furthermore, our analysis on overall intentional binding showed that Libet Clock method revealed the developmental effects on overall intentional binding but Stream of

Letters did not capture this effect. However, it should be noted here that Stream of Letters method captured a developmental trajectory for outcome binding when considered separately. Together with these results and considering the large intentional binding literature using Libet Clock method (Moore & Obhi, 2012) that enables comparisons between studies, we suggest that Libet Clock method might be preferable to use when measuring intentional binding between childhood (9-10) and adulthood (25-28) compared to Stream of Letters.

Intentional binding measured with Stream of Letters and Libet Clock methods showed differences in terms of developmental trajectory they captured. One important issue that might cause this was the predictability versus unpredictability in Libet Clock and Stream of Letters respectively. Clock hand motion is predictable in terms of where it would move in time but the quickly changing random letters are unpredictable. This predictability issue could have affected the results in different ways. First, Libet Clock might be easier due to this predictability but Stream of Letters might require more attention due to the unpredictable letters; hence, Stream of Letters might be more difficult. Indeed, although we did not collect data regarding the reasons, our participants found Libet Clock to be easier than Stream of Letters. This could also be the reason why participants were more stable regarding their judgements (less variability) in Libet Clock compared to Stream of Letters. Consequently, smaller variability might have helped to capture the developmental effect. Second, this predictability versus unpredictability might have created a contextual effect. For example, in adults, we found high intentional binding effect when measured with Libet Clock but we found low intentional binding effect when measured with Stream of Letters. This was also observed for outcome binding. As discussed in the above, adults might have showed predictive over-binding when measured with Libet Clock; however, it is also possible that they did not show this predictive over-binding when there is a contextual unpredictability as seen in Stream of Letters. Indeed, the effects of predictability of the outcomes were shown before where high predictability caused predictive binding but low predictability caused retrospective (inference based) binding (Moore & Haggard, 2008). It is possible that this could be the reason why we observed differential developmental trajectories for intentional binding measured with Stream of Letters and Libet Clock methods. However, it should be noted here that the effect of measurement method’s predictability on intentional binding has not been investigated fully and it should be investigated in the future studies as it might have important effects as seen in the current study.

Furthermore, there were no consistent correlations between intentional binding measured by Stream of Letters and Libet Clock across age groups and binding types. There was only a significant positive correlation in late-adolescent group. This could be surprising since they are suggested to measure the same phenomenon and a strong correlation would be expected. This also supports that, to some extent, they might be measuring different aspects of intentional binding. As discussed above, discrepancies between two measurement methods can be also observed in the developmental trajectories especially when comparing outcome binding. Libet Clock suggests an adolescence-specific developmental trajectory for outcome binding but Stream of Letters suggests a decreasing developmental trajectory from childhood to adulthood. This suggests intentional binding and its developmental trajectory is sensitive to how it is measured and to the task requirements. As discussed above predictability issue might be driving this lack of consistent relationship and differential developmental trajectory between methods which might be underlying the differential developmental trajectory of different cognitive strategies being used based on the task requirements. Hence, future studies are needed to establish which aspects of intentional binding is being measured with these types of methods and this should be considered in the future studies when preferring one method over the other.

Implications of the findings

Our finding that intentional binding shows an adolescent specific developmental trajectory can have variety of implications. First, this finding can be useful for understanding the neural mechanisms of SoA and their development. Future studies focusing on this age range together with imaging techniques can help to understand the neurodevelopment of SoA. Second, this finding can have implications for the legal systems. Our finding suggests a decrease in late-adolescents' agency experiences which could reflect a decreased perceived responsibility for their behaviours. SoA was previously suggested to be associated with criminal responsibility since to hold someone responsible for an act they need to be aware of their agency (Frith, 2014; Haggard & Tsakiris, 2009; Moretto et al., 2011). Although our study does not suggest they lack the complete awareness, it is possible that late-adolescents might not be feeling as much responsible as adults or children do for the behaviours they perform. Hence, this possibility should be further investigated in future research which may help understanding criminal behaviour during adolescence. Third, the developmental trajectory observed in the current study might be helpful to understand when impairments in SoA (i.e.: delusions of control) starts to occur in SoA related neurodevelopmental disorders such as schizophrenia (Frith et al., 2000; Synofzik et al., 2010; Voss et al., 2010). It was shown previously that schizophrenia patients show retrospective over-binding with a specific impairment in predicting the action outcomes (Voss et al., 2010). This might be associated with the lack of a possible developmental shift from retrospective to predictive over-binding from childhood to adulthood with the critical shift occurring during adolescence.

3.6 Study Limitations and Future Directions

There are some limitations to our study. We used an implicit measure, intentional binding to quantify the SoA. However, two levels of SoA have been suggested previously, feeling of agency which is the background feeling of being in charge of the actions, and judgement of agency which is the high-level experience of agency that arise when we make conscious evaluation of the agency (Synofzik et al., 2008). Intentional binding suggested to reflect this low-level feeling of agency (Moore & Obhi, 2012). Therefore, developmental trajectory found in this study might not reflect the developmental trajectory of the judgements (metacognition) of agency. Intentional binding has been considered as the effect of voluntary action on the perceived action outcome temporal relationship and shown to be sensitive to the agency manipulations (for reviews: Hughes et al., 2013; Moore & Obhi, 2012; Moore, 2016). Nevertheless, it should also be noted here that to what extent intentional binding reflects agency experience requires further study since there are conflicting studies suggesting it does not necessarily overlap with explicit agency judgements (see section 1.3.1). Furthermore, this study was not designed to address differential processes underlying intentional binding such as predictive and retrospective processes. Therefore, our proposal about a possible developmental shift from relying on retrospective to predictive processes should be tested in future studies that isolate these processes. It is possible that the developmental changes we observe might have relationship to the development of other factors such as executive functions and attention, and this issue should be investigated in future studies. However, it should be considered that we observed a U-shaped developmental trajectory that would be difficult to reconcile with attention and executive function development. Also, we only compared two mental chronometry methods of measuring intentional binding. Hence, other methods such as interval estimation might have its advantages such as focusing on the interval in between action and outcome instead of focusing on isolated timings of the events as seen in mental chronometry methods. However, interval estimation methods do not allow measuring action and outcome binding separately which we found to show different developmental trajectory. Comparison of these two different approaches can be considered in future studies. In addition, the auditory stimulus used as the action outcome did not have any specific value for the participants. Therefore, the developmental trajectory observed might be different when socially relevant, emotional or rewarding stimulus is used. This is especially important for adolescence where we see an increased responsivity to both rewarding and aversive stimulus (Casey, 2015). Hence, developmental trajectory of SoA when the outcomes of actions have value might be an important avenue for the future research.

3.7 Conclusions

The current study investigated SoA in the transition from childhood to adulthood for the first time. It revealed the developmental trajectory of intentional binding phenomenon that has been suggested to reflect agency experience, and the differences between two mental chronometry methods being used to measure intentional binding in the literature. Intentional binding measured with Libet Clock showed an adolescent specific developmental trajectory with exaggerated binding in children and adults and a decrease until late-adolescence. This might be possibly underlined by retrospective over-binding in children and predictive over-binding in adulthood with a balance being achieved in late-adolescence. Comparisons between the two methods suggest that Libet Clock might be advantageous for measuring intentional binding from childhood to adulthood since it is more stable and reported to be easier compared to Stream of Letters. Overall this study suggests critical importance of the adolescence in the development of intentional binding effect and consequently SoA. These results can have implications for the future research aiming to understand the neurodevelopment of SoA and schizophrenia, a neurodevelopmental disorder with an impaired SoA.

Chapter 4

4. Neural correlates of implicit agency during the transition from adolescence to adulthood: An ERP study

Abstract

Sense of agency (SoA), the experience of being in control of our voluntary actions and their outcomes, is a key feature of normal human experience. Fronto-parietal brain circuits that are associated with SoA undergo a major final maturational process during adolescence, which consequently can provide a window for understanding neural mechanisms and development of SoA. Based on this, using EEG we investigated neural correlates of an implicit measure of SoA, intentional binding in mid-adolescents: 13-14, late-adolescents: 18-20 and adults: 25-28 years-old. We used an intentional binding task where participants pressed a button (action) that delivers a tone (outcome) after a small delay and reported the time of the tone using Libet clock. This action-outcome condition alternated with a no-action condition where an identical tone was triggered by a computer. EEG data were analysed time-locked to the action and tone. Behavioural results showed greater outcome binding, perceived temporal linkage of outcomes to actions, in mid-adolescents compared to adults, with late-adolescents in between. Consistent with this, ERP results revealed a greater auditory P2 attenuation in mid-adolescents compared to older participants when the tone was self-triggered. This enhanced attenuation effect decreased with age showing similarity with outcome binding. In contrast, neither N1 nor readiness potential showed any developmental effects. Interestingly, in the mid-adolescent group only, greater outcome binding scores were associated with greater P2 attenuation and smaller negativity in the late readiness potential. Our findings suggest a greater experience of implicit agency, which may be mediated by a neural over-attenuation of action outcomes and over-reliance on motor preparation in mid-adolescents, which we found to become adult-like in the late-adolescence.

4.1 Introduction

The previous study (Chapter 3) found that there was an adolescent-specific developmental trajectory for intentional binding, suggesting that the transition from adolescence to adulthood can be a critical period for the development of SoA. Showing a U-Shaped curve, intentional binding, perceived temporal linkage of actions and outcomes, was greatest in childhood and steadily decreased in mid-adolescence and late-adolescence and increased to about childhood level in adulthood again. The decrease of intentional binding reached its lowest point in late-adolescents which was significantly smaller compared to younger and older age-groups. Previous chapter argued that the developmental trajectory observed in the previous study might be a result of a developmental shift from relying on retrospective processes (inference based) in childhood to relying on predictive processes in adulthood with a balance of using both being achieved in late-adolescence. It suggested that the reliability of the predictive processes might be low in younger age groups since underlying neural basis is still not fully mature causing the use of retrospective processes more. Whereas, by adulthood, this would switch to a reliance on predictive processes due to the maturation of the frontal areas that are associated with predictive processes (Asato et al., 2010; Gogtay et al., 2004; Moore et al., 2010; Sowell, Thompson, Holmes, Jernigan, et al., 1999; Wolpe et al., 2014). Therefore, current study aimed to investigate this idea by examining ERP components that are associated with the predictive processes, especially predictions of the outcomes (readiness potential, N1 and P2 attenuation) in the transition from adolescence to adulthood. In this study, we only focused on the outcome binding, perceived temporal shift of outcomes towards actions, since the developmental trajectory observed in previous chapter was driven by outcome binding. Below, I will give a summary of the literature that led to this investigation.

One way of measuring SoA is by the use of intentional binding phenomenon (discussed in section 1.3.1). Intentional binding refers to the perceived contraction of subjective time between a voluntary action and its outcome (Haggard et al., 2002). It represents the perceived temporal linkage between actions and outcomes. Overall intentional binding measure consists of action and outcome binding which is perceived shift of action and outcome towards one another respectively. Previous studies have shown that action and outcome binding are mediated by different processes in the brain (discussed in section 1.3.1). Disruptions of the pre-supplementary motor area (pre-

SMA, an area related to action initiation and efferent copy generation) using transcranial magnetic stimulation was found to produce a weakening of outcome binding but not action binding (Moore et al., 2010). Accordingly, the early readiness potential (RP, bereitschaftpotential) which is associated with the preparatory cortical activity in the pre-SMA that precedes the actions was shown to be closely correlated with outcome binding but not action binding (Jo et al., 2014). These findings suggested different mechanisms for action and outcome binding together with an importance of the top-down predictive mechanisms on the sensory processing of the outcome (Roussel et al., 2013; Waszak et al., 2012).

Another phenomenon that has been associated with SoA is sensory attenuation (see section 1.3.2). Sensory attenuation refers to a decrease in the perceived intensity of a self-generated stimulus (outcome) compared to an externally-generated stimulus (Blakemore et al., 2000). For instance, self-generated tactile stimulation is perceived less intense compared to externally generated tactile stimulation. This effect has also been observed as the attenuation of neural responses. For example, it has been found that N1 auditory event related potential (ERP) component to a self-generated auditory stimulus was attenuated compared to an externally generated auditory stimulus (Aliu et al., 2009; Baess et al., 2008; Schafer & Marcus, 1973). Although sensory attenuation has been mostly studied by focusing on N1 attenuation, this attenuation effect has also been observed in the auditory P2 ERP which is a positive peak around 200 ms following the N1(Behroozmand et al., 2011; Ford et al., 2001; Knolle et al., 2012; Sanmiguel et al., 2013; Schafer & Marcus, 1973; Sowman et al., 2012). Furthermore, it has been previously shown that P2 attenuation, but not N1, might be related to the agency judgements in adults (Timm et al., 2016). Sensory attenuation has been suggested to be important for differentiating self-generated sensory consequences from externally generated ones.

Both intentional binding, specifically outcome binding and sensory attenuation are thought to be driven by a "pre-activation" process (Waszak et al., 2012; Wolpe et al., 2013) (discussed in section 1.4.4). According to this, based on the efferent copy of the motor command, predicted action outcome pre-activates the neural representation of the forthcoming outcome, and the increased predictive baseline activity cause an attenuation of the cortical response to the outcome (also see the comparator model, section 1.4.2). Furthermore, this increased predictive activity helps the perception of the outcome to reach the perceptual threshold faster and consequently to be perceived as earlier in time (as measured by outcome binding) than when it is not predicted. In line with this, fronto-parietal interactions have been suggested to underline SoA (Haggard, 2017). This neural network includes, the dorsolateral prefrontal cortex (DLPFC) (Khalighinejad et al., 2016; Wolpe et al., 2014) involved in action selection (a process that is closely tied to the intended outcomes), pre-SMA/SMA that is involved in action initiation and preparation including sending efferent copy to parietal regions (Haggard & Whitford, 2004; Moore et al., 2010), and angular gyrus (a parietal cortex structure) that is involved in action and outcome monitoring (Khalighinejad & Haggard, 2015; Voss, Chambon, Wenke, Kühn, & Haggard, 2017).

This fronto-parietal network subserving SoA undergoes substantial structural and functional connectivity changes during adolescence (Asato et al., 2010; Gogtay et al., 2004; Luna, Padmanabhan, & Hearn, 2010; Sowell et al., 2003). Dramatic maturational changes were shown to occur in parietal regions from childhood (mean age: 8.6) to adolescence (mean age: 14) (Sowell et al., 1999) and in frontal regions from adolescence to adulthood (mean age: 25.6) (Gogtay et al., 2004; Sowell et al., 1999). In addition, prominent structural and functional differences from adolescence to adulthood have been also observed in the striatum (Luna et al., 2001; Sowell et al., 1999), a key region that is involved in initiating and modulating voluntary movement (Alexander & Crutcher, 1990), and possibly involved in SoA. These studies suggest that adolescence might be a critical period for the development of SoA. Indeed, we found an adolescent specific developmental trajectory for intentional binding in the previous study (Chapter 3) suggesting the transition from adolescence to adulthood might be an important period for key changes in SoA.

Consequently, the present study investigated implicit SoA as indexed by intentional binding during the transition from adolescence to adulthood in mid-adolescents (13-14), late-adolescents (18-20) and adults (25-28). This study specifically focused on the outcome binding component of overall intentional binding because our developmental effect on intentional binding was driven by the changes in outcome binding, which was also suggested to be underlined by a top-down predictive mechanism (Moore et al., 2010; Waszak et al., 2012) that might show a more protracted development. To that end, we designed an intentional binding task to examine: 1) behavioural outcome binding effect, 2) auditory ERP components that are associated with sensory attenuation (N1 and P2) and 3) the RP, which is related to action preparation processes. In so doing, we were particularly interested in whether the neural components associated with action outcome processing (N1 and P2 attenuation) and/or those related to voluntary action preparation (RP) would be associated with the developmental changes in outcome binding. We predicted that modulations of the sensory outcome processing by top-down predictive mechanisms would improve with age due to the maturing fronto-parietal network that underlines SoA. This would be reflected by an observed increase in sensory attenuation, as well as increasing association of the predictive processes underlined by motor preparation (RP) in implicit SoA in the transition from adolescence to adulthood.

4.2 Method

4.2.1 Participants

Sixty right-handed healthy participants took part. There were 20 participants in each age-group with the same sex ratio (10 females in each group). These age-groups were mid-adolescents (13-14 years-old, mean =13.5, SD =0.5), late-adolescents (18-20 years-old, mean = 18.9, SD =0.8) and adults (25-28 years-old, mean = 26.4, SD =0.99). They were compensated with £10 for their time. Participants reported normal or corrected to normal vision and hearing, and no history of psychiatric/neurological conditions. All participants (and their parents if they were under 18 years-old) gave informed consent before the experiment started. This study was approved by the University of Sheffield, Department of Psychology Ethics Committee.

4.2.2 Materials and Experimental Procedure

A PC running PsychToolbox 3 (Kleiner et al., 2007) controlled the experimental events and recorded data. For the experimental task, participants sat about 90 cm away from the screen (144Hz, 24-inch, iiyama ProLite GB2488HSU-B1) in a dimly lit room. Participants made button presses using a custom build, silent, grip-handle button device connected to an Arduino micro-controller (Figure 4.1A, < 2 ms latency, Schubert et al., 2013). This silent button was used to avoid the immediate auditory feedback (i.e., a clicking sound) upon button press since it would be perceived as the action outcome. The auditory stimulus serving as the action outcome (100 ms duration, 1000 Hz, ~85 dB) was presented using air tube in-ear headphones (Kinden radiation-free headset) to minimise electrical interference with EEG recording.

During our intentional binding task (Figure 4.1), participants were asked to watch a Libet Clock, which involved a clock hand (12 mm) rotating on an analogue clock face. After the start of each trial, the clock hand appeared at a random time (1-2 s) and a random position, and started rotating. It completed one rotation in 2520 ms and stopped at a random interval (1-2 s) after the event of interest occurred. Participants were instructed to report the position of the clock hand at the time when they heard the beep sound in two different conditions: Action-Beep and Beep-Only. In *Action-Beep* condition participants pressed the button with their right thumb at a time of their own choosing, although they were instructed not to press the button earlier than one full rotation (Figure 4.1A). They were also instructed to make spontaneous button presses instead of trying to react to a pre-chosen position. Participants heard the auditory stimulus, the beep sound 450 ms after their button press. This delay duration was chosen to avoid motor contamination on auditory ERPs (Hughes et al., 2013a; Hughes & Waszak, 2011; Poonian et al., 2015). An alternative way of controlling for motor contamination that is commonly used in sensory attenuation literature is including an action only condition where participants only make a motor action which does not lead to an outcome and subtracting this activity from other conditions to control for motor contamination (e.g. Baes et al., 2008). However, including such condition would require substantial increase of trial number and experiment duration which might be difficult for special populations such as adolescents. Furthermore, to my knowledge, this method has not been used together with Libet Clock method. When this method is involved it is possible that participants might make judgements about the time of their actions in action only conditions even though they are not asked to do so. Hence, subtracting this activity from other condition may not only subtract motor activity but also activity that is related to some cognitive functions. Therefore, in the current study we used longer delay duration to avoid motor contamination. The clock hand continued rotating for a random duration (1-2 s) and disappeared. Participants reported the time of hearing beep sound by typing via a number pad at the end of each trial. In the *Beep-Only* condition (Figure 4.1B) participants performed the same task except that the beep was triggered by the computer at a random time between 3 to 8 s after the trial onset (Cavazzana et al., 2014; Haggard et al., 2002). There were four blocks in each condition. Each block contained 33 trials resulting in 132 trials in total for each condition. Participants performed each block in an alternating fashion between conditions and the order of the starting condition was counterbalanced. Participants had a break between blocks. Prior to the start of the experiment participants completed the verbal and matrix reasoning parts of the Wechler Abbreviated Scale of Intelligence (WASI).

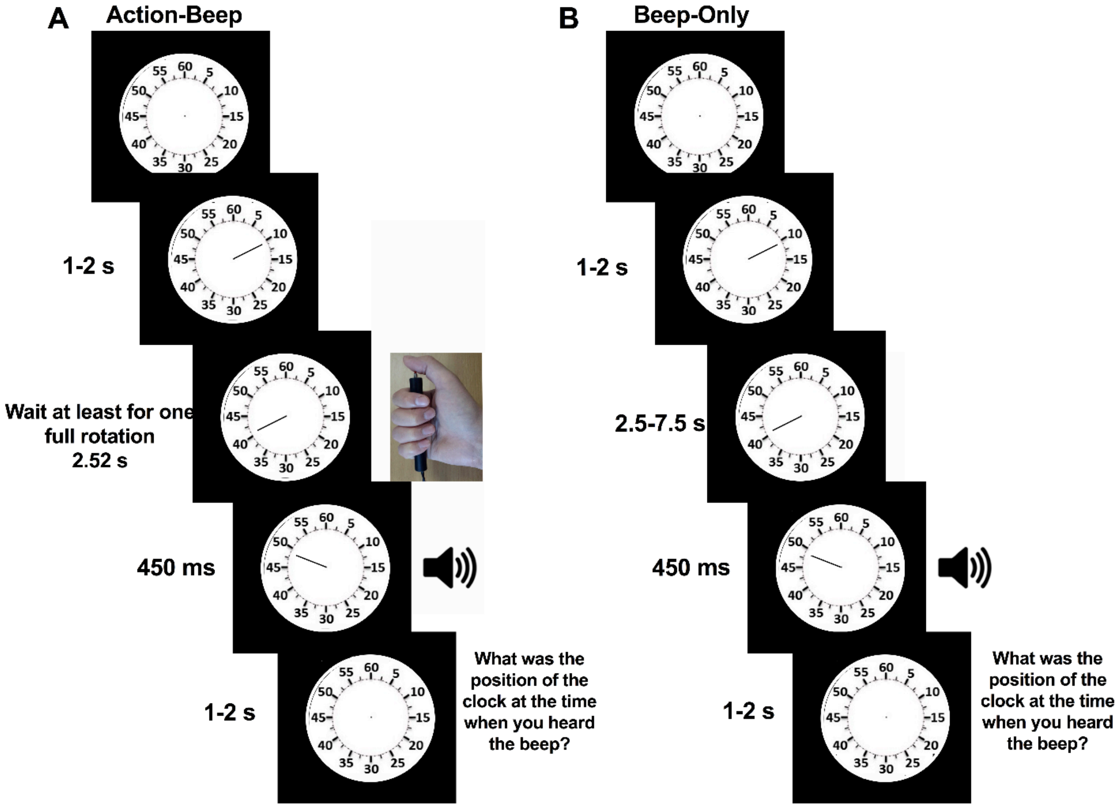

Figure 4.1. *Intentional binding task.* **A**. *Action-Beep condition. Participants heard an auditory beep sound (100ms, 85db, 1000 Hz) which was evoked as a consequence of their action, a button press.* **B**. *Beep-Only condition. Participants heard the same beep sound, which was triggered by the computer at random intervals. After both conditions participants were asked to report the position of the clock hand at the time when they heard the beep sound. Time and the size of the clock is not to scale.*

4.3 EEG Data Acquisition and Pre-Processing

The BioSemi ActiveTwo system with 64 Ag/AgCI active electrodes (placed according to international 10-20 system) was used for EEG recordings (BioSemi B.V, Amsterdam, Netherlands). Electrode offsets were kept below ±20 µV and EEG data were recorded with 2048 Hz sampling rate and down-sampled offline to 512 Hz using BioSemi Decimator. EEG analysis was conducted using EEGLAB (Delorme & Makeig, 2004) with ERPLAB plug-in (Lopez-Calderon & Luck, 2014). EEG data were imported first referenced to Cz and re-referenced to average. Data were then 0.01 Hz high-pass filtered. This high-pass filter was set relatively low to avoid eliminating slow wave activity related to readiness potential (Poonian et al., 2015). Line noise was reduced using CleanLine plugin (Mullen, 2012). Continuous data were visually inspected to remove bad channels and bad sections (i.e.: muscle and movement artefacts) except data on eye blinks and eye movements. Following this, EEG data relating to eye blinks and eye movements were corrected using independent component analysis (ICA) (Delorme & Makeig, 2004). Finally, removed bad channels were interpolated (number of channels interpolated: mid-adolescents: mean = 6.4, SD = 3.0; late-adolescents: mean = 3.5, SD = 2.4; adults: mean = 3.8, SD = 3.0).

We obtained ERP epoch datasets 1) time-locked to auditory stimulus (auditory ERPs) and 2) time-locked to button-press (readiness potential). For auditory ERPs, epochs were created from -100 ms to 1000 ms relative to auditory stimulus onset with a pre-stimulus baseline correction. For readiness potential, epochs were created from -2500 ms to 1000 ms relative to button press (for Beep-Only condition it was relative to beep onset since there was no action) with a 200 ms baseline correction from -2500 to -2300 ms (Jo et al., 2014). Epochs where participants pressed the button earlier than one full rotation of the clock were removed from the analysis (Jo et al., 2014). Finally, epochs that were over ±100 μV threshold were removed (Hughes et al., 2013a). We excluded participants who did not have at least 60 epochs in either condition from further analyses. Based on this, all participants were included for the auditory ERP analysis; however, four mid-adolescents and one adult were removed from our readiness potential analysis. Average number of epochs that were included in each specific ERPs within each condition is as follows. For auditory ERPs, in mid-adolescents, action beep: 112.7 (SD = 13.73), beep only: 106.3 (SD = 17.5); in late-adolescents, action beep: 122.2 (SD = 7.3), beep only: 119.8 (SD = 12.2); in adults, action beep: 122.1 (SD = 10.5), beep only: 119.5 (SD = 15.7). For readiness potential, in mid-adolescents, action beep: 97.3 (SD = 17.2), beep only: 96.5 (SD = 14.2); in late-adolescents, action beep: 104.9 (SD = 18.0), beep-only: 110.6 (SD = 18.5); in adults, action beep: 113.2 (SD = 15.8), beep only: 111.7 (SD = 15.7).

4.4 Data Analysis

4.4.1 Behavioural Data: Outcome Binding

The first three trials of each block were considered as practice trials, and they were excluded from the analysis (Cavazzana et al., 2014). Average judgement errors (JEs) were calculated by subtracting the actual time of the event (beep onset) from the reported time of the event in each condition (Action-Beep, Beep-Only). For all groups, trials with JEs above and below 2 SD from the average of each block in each condition were excluded from further analysis (Mid-Adolescents: 3.9%, Late-Adolescents: 4.1% and Adults: 4.0% of data). Average JEs for each block and then for each condition were calculated. To calculate outcome binding for each individual, we subtracted averaged Beep-Only JEs from averaged Action-Beep JEs. Hence, perceived temporal shift of the beep from Beep-Only condition to the Action-Beep condition represents outcome binding, with greater outcome binding representing greater effect of agency on temporal action-outcome relationship.

4.4.2 ERPs time-locked to auditory stimulus: N1 and P2

For each participant, averaged ERPs to the auditory stimulus were created within each condition and 30 Hz low-pass filter was applied before quantifying ERPs. Our analysis was conducted on the frontocentral and cetroparietal electrodes (FC3, FCz, FC4, C3, Cz, C4, CP3, CPz and CP4) as in Poonian et al. (2015). Local peak amplitude was used to quantify the auditory ERPs due to the latency differences between conditions (Luck, 2014, p.285) which makes it difficult to set a narrow time window for the mean amplitude (e.g.: 80-105 ms for N1 as in Poonian et al., 2015). Therefore, N1 was quantified as the negative local peak between 75 and 175 ms, and P2 was quantified as the positive local peak between 140 and 240 ms. These time windows were determined by grand-grand averaging all groups and conditions. Then, each participants' ERPs in each condition and age groups were quantified as the local peak within this time window. This approach allowed us to set wider time windows to capture N1 and P2 together with reducing the effects of latency differences.

4.4.3 ERPs time-locked to button-press: early and late readiness potential

Readiness potential (RP) involves early and late parts that can be distinguished based on their timing and topography. Early RP is a negative ongoing activity that starts around 2 s before a voluntary movement which is thought to be related to intentions to move, and is generated in the pre-SMA/SMA. By contrast, late RP starts about 500 ms before the voluntary movement which is thought to be more specific motor preparation activity and generated in the M1 and pre-motor cortex (Shibasaki & Hallett, 2006). A previous intentional binding study showed that Early RP but not Late RP was associated with outcome binding (Jo et al., 2014). Therefore, we analysed early and late RP separately to be able to investigate these constituents. We first averaged FCz, Cz and CPz to increase signal to noise ratio as in Jo et al. (2014). We calculated early and late readiness potential slope following the same procedure used by Jo et al. (2014). Early readiness potential slope was quantified by calculating the mean amplitude between -2500 and -2300 ms (which was baseline; hence, equal to 0) and subtracting it from the mean amplitude between -1000 and -800 ms, then dividing this difference with the duration of the early readiness potential (1500 ms). Similarly, late readiness potential slope was quantified by calculating the mean amplitude between -700 and -500 ms, and subtracting it from the mean amplitude between -200 and 0 ms, then dividing this difference by the duration of the late readiness potential (500 ms). Therefore, the amplitude increase for both early and late readiness potential from their relative onset was divided by their relative durations.

4.4.4 Statistical Analysis

A univariate ANOVA for outcome binding and mixed model ANOVAs for ERP analysis were used with the relevant factors for each analysis. Greenhouse-Geisser correction was applied whenever the homogeneity of variance was violated. Significant interactions were followed up with pairwise comparisons. Bivariate correlations (Pearson) were used to investigate the relationship between Outcome-Binding, N1-P2 attenuation, and Early-Late readiness potential. Correlations were conducted within each age-group. Benjamini-Hochberg procedure for multiple comparisons was applied (Benjamini & Hochberg, 1995).

4.5 Results

4.5.1 Behavioural Results

4.5.1.1 IQ Differences between Groups

A one-way ANOVA showed that there was a significant age-group effect on participants' IQ scores measured with Wechler Abbreviated Scale of Intelligence (WASI) [F (2, 58) = 3.94, $p = 0.025$]. Late-adolescents (mean = 109.5, SD = 8.7) showed lower IQ scores in comparison to both mid-adolescents (mean = 115.5, SD = 7.9) and adults (mean =116.4, SD = 8.5). Therefore, we included IQ scores as a covariate in further analyses. As suggested previously, IQ covariate was mean centred to avoid from altering the main effect of the repeated measure variables (Delaney & Maxwell, 1981; e.g.: Redshaw, Vandersee, Bulley, & Gilbert, 2018).

4.5.1.2 Outcome Binding

A univariate ANOVA was conducted to investigate the effect of age-group (mid-adolescents, late-adolescents and adults) on outcome binding scores. There was a trend level age-group effect [F (2, 55) = 2.872, $p = 0.065$, $\eta p^2 = 0.095$] (Figure 4.2A). Pairwise comparisons showed that mid-adolescents had greater outcome binding than adults ($p = 0.02$), but late-adolescents did not significantly differ from both mid-adolescents and adults ($p > 0.2$).

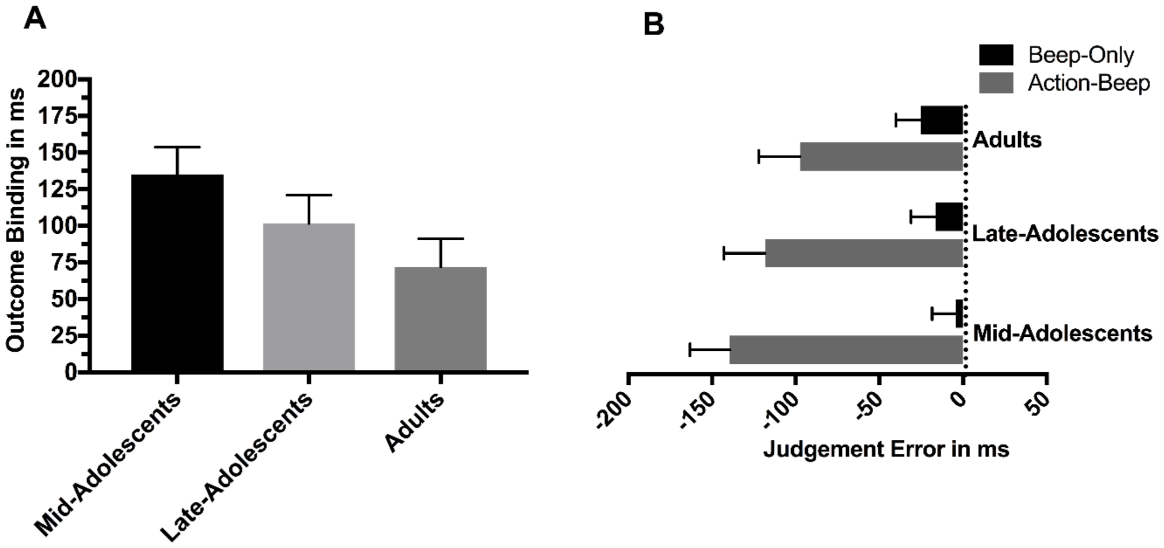

Figure 4.2. A. Means for outcome binding scores in each group. Outcome binding was calculated as the difference of Judgement Errors between Beep-Only and Action-Beep condition. There was a trend level age-group effect (p = 0.065). Values converted into positive for illustration purpose. ***B.*** Means for the judgement errors (the time difference between actual beep time and reported beep time) in Beep-Only and Action-Beep conditions for each Age-Group. Here, '0' represents the actual onset time of the beep and bars shows the reported beep time on average for each group and condition. As can be seen, participants reported beeps earlier in Action-Beep compared to Beep-Only condition. There was a main effect of condition (p < 0.001). Error bars represent the Standard Error of the Mean (SEM)

We then investigated whether the perceived time of the beep shifted towards action (button press) in the action beep condition (outcome binding) by conducting a mixed model ANOVA on participants' judgement errors (JEs) with condition (Action-Beep vs. Beep-Only) as a within-subject variable and age-group as a between-subject variable (Figure 4.2B). There was a main effect of condition [*F* (1, 55) = 92.508, $p <$ 0.001, $\eta p^2 = 0.627$] suggesting that they reported the timings of the beep earlier towards action in the Action-Beep compared to Beep-Only condition (Figure 4.2B, $p < 0.001$). That is, perceived time of the beep was earlier in Action-Beep compared to Beep-Only condition. There was also a trend level of interaction between age group and condition [*F* (2, 55) = 2.87, $p = 0.065$, $\eta p^2 = 0.095$]. Pairwise comparisons showed that beep times were reported significantly earlier in Action-Beep condition compared to Beep-Only condition in all age groups, suggesting that outcome binding effect was observed in all age groups ($p < 0.001$). However, there was no significant difference between age groups within each condition ($p > 0.2$) and no significant main effect of age-group on the Judgement Errors [*F* (2, 55) = 0.09, $p = 0.91$]. See Table 4.1 for mean Judgement Error and outcome binding scores.

Table 4.1. *Mean outcome binding scores and judgement errors in milliseconds. Standard errors of the mean presented in bracket*

	Outcome Binding	**JE Beep-Only**	**JE Action-Beep**
Mid-Adolescents	-135 (18.5)	-4 (14.1)	-139 (23.7)
Late-Adolescents	-101 (19.2)	-16 (14.6)	-118 (24.6)
Adults	-72 (19.1)	-25 (14.6)	-97 (24.5)

Note: Negative Judgement Errors (JE) means that participants reported the time of the beep earlier than it was; hence, an anticipatory error. Outcome binding was calculated as the mean JE difference between Beep-Only and Action-Beep.

4.5.2 ERP Results

4.5.2.1 N1 attenuation

A mixed model ANOVA was conducted to investigate the effect of age-group on N1 attenuation with electrodes (9 electrodes around CZ) as within subject variable and age-group as between subject variable. There was a significant main effect of electrode. As seen in Figure 4.3A largest N1 attenuations were observed over FCz and Cz [F (3.309, 182.015) = 20.01, $p < 0.001$, $\eta p^2 = 0.267$]. However, there was no significant main effect of age-group [F (2, 55) = 0.899, $p = 0.413$] or its interaction with electrodes [F (6.619, 182.015) = 1.487, $p = 0.178$].

We then examined whether we observed attenuated N1 amplitude in Action-Beep compared to Beep-Only condition (sensory attenuation effect) as reported in the literature by conducting a mixed model ANOVA on N1 amplitudes with condition as a within-subject and age-group as a between-subject variables. ERP waveforms for N1 in central electrodes and topographical maps can be seen in Figure 4.4. Significant main effect of condition confirmed N1 attenuation to self-generated beep, since N1 amplitude was smaller in Action-Beep condition than Beep-Only condition [F (1, 55) = 101.54, $p < 0.001$, $\eta p^2 = 0.649$]. There was no significant Condition x Age-Group x Electrode interaction [F (6.619, 182.015) = 1.487, $p = 0.178$], suggesting that the effect of condition was not significantly different across age groups and electrodes (see supplementary Table 1 for mean amplitudes). We found a significant interaction between condition and electrode [F (3.309, 182.015) = 20.01, $p < 0.001$, $\eta p^2 = 0.267$]. Pairwise comparisons showed that there was a significant N1 attenuation to the self-generated beeps in all electrodes ($p < 0.001$) and N1 amplitude was highest in frontocentral electrodes FCz and Cz for both conditions.

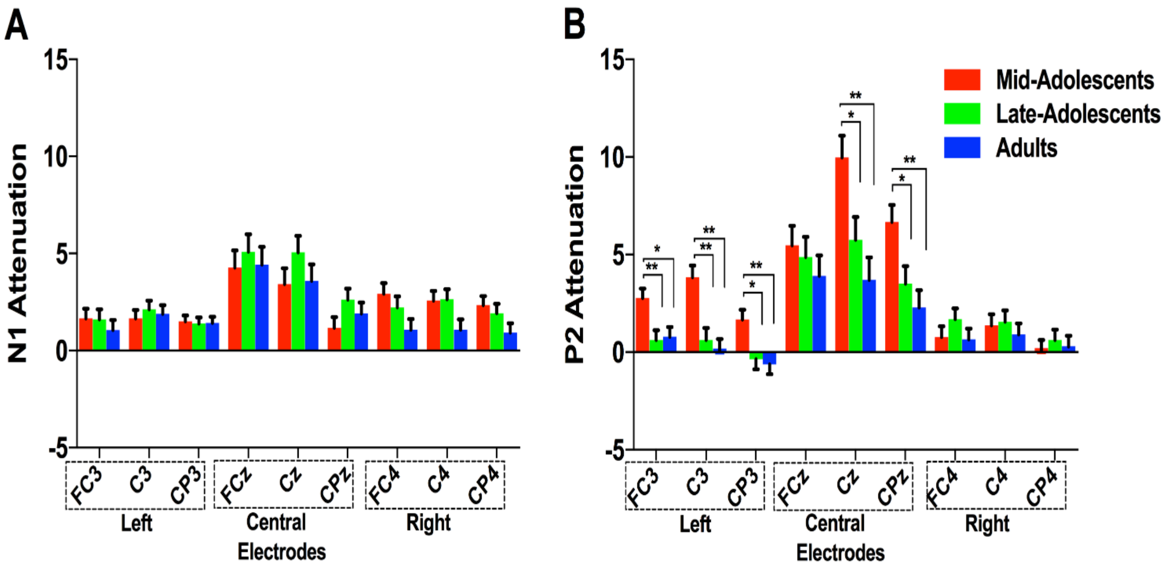

Figure 4.3 Auditory N1 and P2 attenuation. **A)** Mean N1 attenuation for 9 electrodes around Cz. Although there was a significant N1 attenuation effect ($p < 0.001$), it did not significantly differ between the three age-groups ($p = 0.178$). N1 attenuation scores were converted into positive for illustration purpose **B)** Mean P2 attenuation for 9 electrodes around Cz. Mid-Adolescents showed significantly greater P2 attenuation than both late-adolescents and adults mostly in left electrodes which were contralateral to the action hand and central electrodes. N1 and P2 attenuation was calculated as the amplitude difference between Beep-Only and Action-Beep condition. Error bars represent the standard errors of the means (SEM). $^*p < 0.05$, $^{**}p < 0.005$

4.5.2.2 P2 attenuation

A mixed model ANOVA was conducted on P2 attenuation with electrode (9 electrodes around CZ) as a within-subject variable and age-group as a between-subject variable. There was a significant main effect of age-group [$F(2, 55) = 5.634$, $p = 0.006$, $\eta p^2 = 0.170$] and its interaction with electrode [$F(6.869, 188.909) = 4.41$, $p < 0.001$, $\eta p^2 = 0.138$]. Pairwise comparisons showed that mid-adolescents had significantly greater P2 attenuation compared to both late-adolescents and adults in mostly left (FC3, C3, CP3) which was contralateral to the action hand and central (including Cz, CPz) electrodes ($p < 0.016$) but not in right-side electrodes ($p > 0.2$) (FC4, C4, CP4) (see Figure 3B). There was no significant difference between late-adolescents and adults in any electrodes ($p > 0.2$). There was a significant main effect of electrode as shown in Figure 4.3B. Relatively greater P2 attenuation was observed over central electrodes: FCz, Cz and CPz [$F(3.435, 188.909) = 46.309$, $p < 0.001$, $\eta p^2 = 0.457$].

To further investigate if attenuation effect on P2 amplitude was evident (significant attenuation effect on P2 amplitude from Beep-Only to Action-Beep) in all age groups, we performed a mixed model ANOVA on participants' P2 amplitudes with condition as a within subject and age-group as a between subject variables. There was a main effect of condition where P2 amplitude significantly decreased from Beep-Only to Action-Beep condition [F (1, 55) = 68.718, $p < 0.001$, $\eta p^2 = 0.555$] suggesting P2 attenuation to the self-generated beeps. There were also significant main effects of age-group [F (2, 55) = 7.362, $p< 0.005$, $\eta p^2 = 0.211$] and electrode [F (3.025, 166.375) = 123.265, $p < 0.001$, $\eta p^2 = 0.691$], and a significant Condition*Age-Group*Electrode interaction [F (6.869, 188.909) = 4.41, $p < 0.001$, $\eta p^2 = 0.138$] (see Supplementary Table 2 for mean amplitudes). Pairwise comparisons showed that mid-adolescents showed a significant decrease of P2 amplitude from Beep-Only to Action-Beep condition in mostly left (FC3, C3 and CP3) and central electrodes (FCz, Cz and CPz) and C4 ($p < 0.016$). In late adolescents, this decrease of amplitude was significant in right (FC4, C4 but not in CP4) and central (FCz, Cz and CPz) electrodes ($p < 0.008$). Finally, in adults the decrease of amplitude from Beep-Only to Action-Beep condition was significant only in central electrodes (FCz, Cz and CPz; $p < 0.013$). Overall, these results suggest a P2 attenuation in our experiment mostly in central electrodes together with some lateralisation differences in mid- and late-adolescents. In general, P2 amplitudes were highest in central electrodes in all age-groups in both conditions. ERP waveforms for P2 in central electrodes and topographical maps can be seen in Figure 4.4. Mid-Adolescents had significantly larger P2 amplitudes than both late-adolescents and adults in Beep-Only condition in left and central electrodes ($p < 0.005$). This was similar in Action-Beep condition for central electrodes but not for the left side electrodes where mid adolescents did not significantly differ from both late-adolescents and adults ($p > 0.05$). In both conditions, P2 amplitude did not significantly differ between late-adolescents and adults ($p > 0.05$).

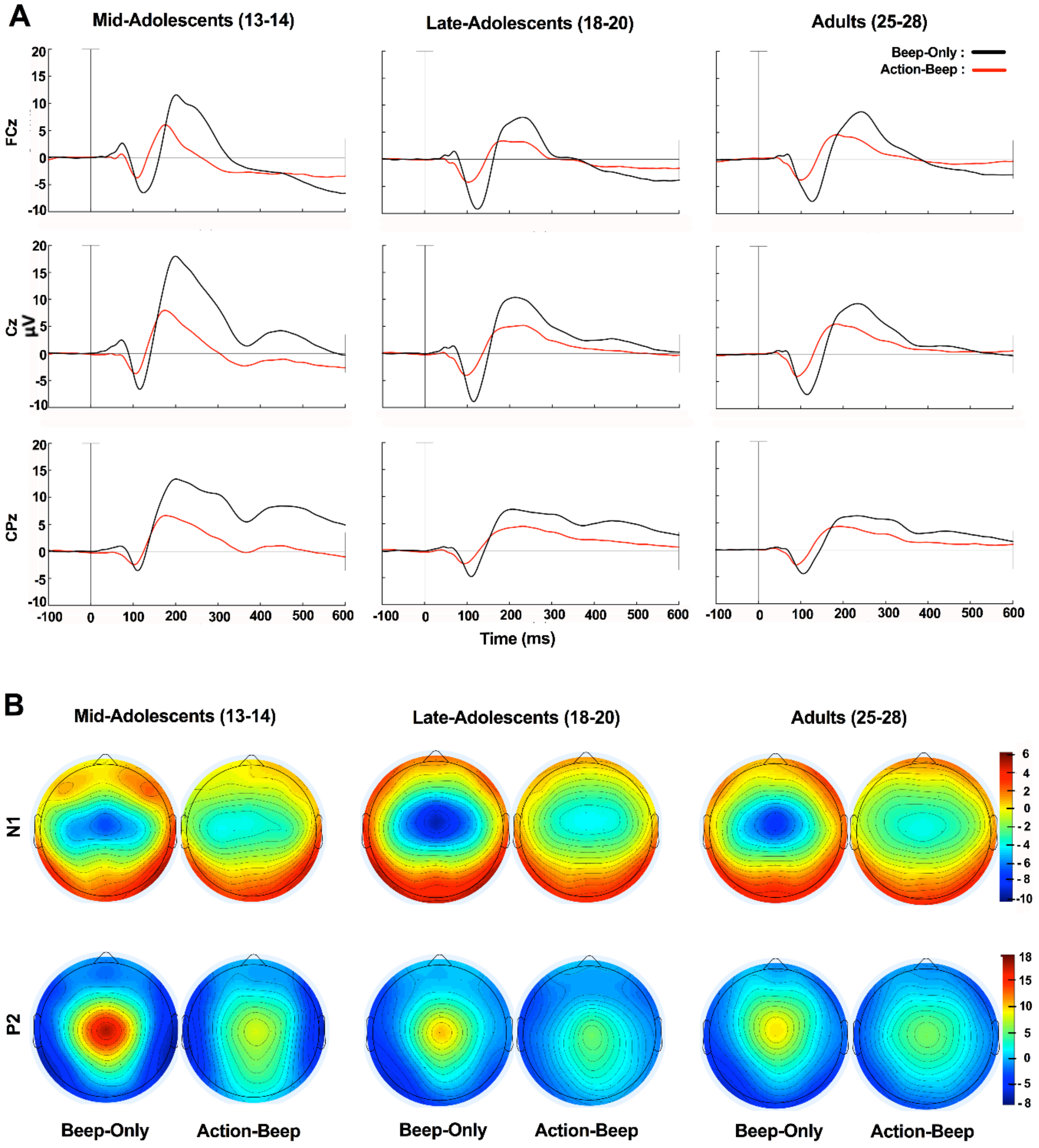

Figure 4.4 A) *Group averaged auditory evoked potential N1 (negative local peak between 75-175 ms) and P2 (positive local peak between 140-240ms) waveforms at central electrodes where they were greatest for the Beep-Only and Action-Beep conditions in all age groups.* **B)** *Topographical maps for N1 and P2 based on the peak latency at CZ where the largest sensory attenuation effect was observed.*

4.5.2.3 Readiness Potential (RP)

Group-averaged readiness potential waveforms and topography maps can be seen in Figure 4.5. A mixed model ANOVA on readiness potential slopes was conducted with Condition (Action-Beep vs. Beep-Only) and Time (Early vs. Late readiness potential) as within-subject factors and Age-Group as a between-subject factor (see Table 4.2). We did not find a significant main effect of the age-group or its interactions with other variables ($p > 0.25$). There were main effects of condition [F (1, 50) = 32.139, $p < 0.001$, $\eta p^2 = 0.391$] and time [F (1, 50) = 6.923, $p = 0.011$, $\eta p^2 = 0.122$], and their interaction [F (1, 50) = 9.848, $p = 0.003$, $\eta p^2 = 0.165$]. Pairwise comparisons revealed that both Early and Late readiness potentials were significantly larger in Action-Beep condition [F (1, 50) = 14.286, $p < 0.001$, $\eta p^2 = 0.222$] than Beep-Only condition [F (1, 50) = 29.956, $p < 0.001$, $\eta p^2 = 0.375$]. Furthermore, there was a significant increase in the negativity from Early to Late part of the readiness potential only in Action-Beep condition [F (1, 50) = 10.516, $p = 0.002$, $\eta p^2 = 0.174$] but not in Beep-Only condition [F (1, 50) = 0.025, $p = 0.875$].

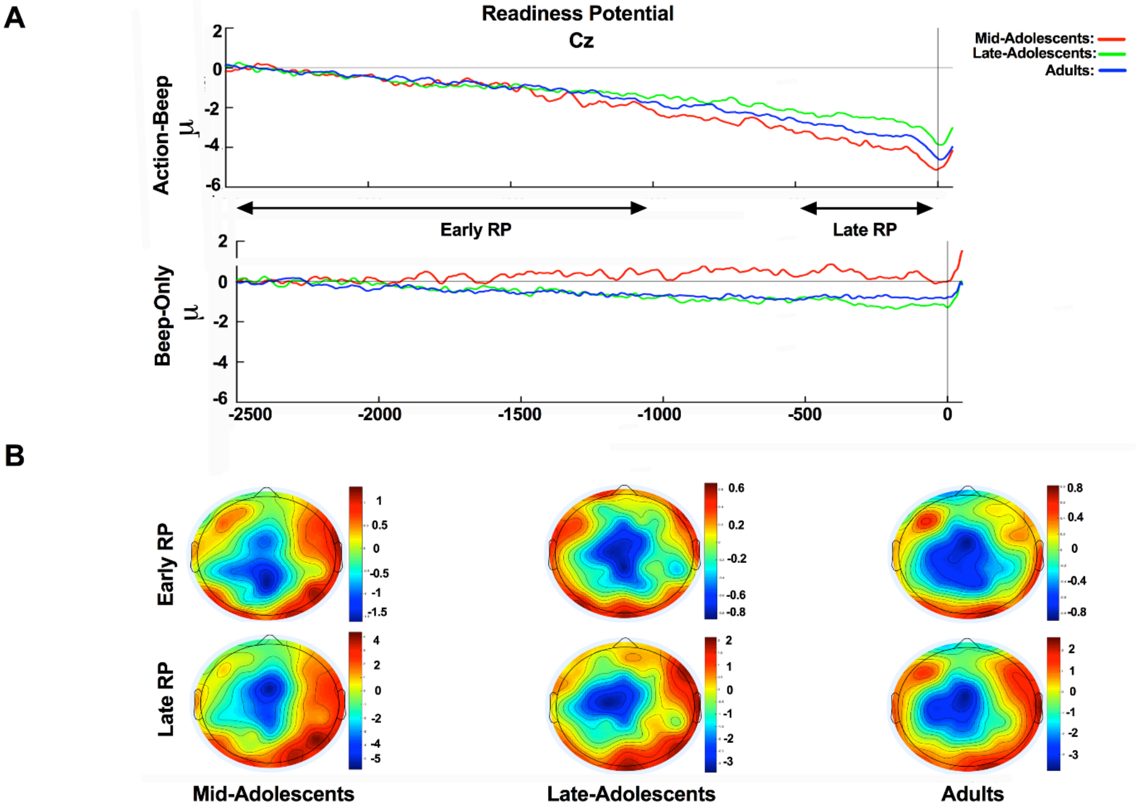

Figure 4.5. **A.** *Early and late RP for all age groups in Beep-Only and Action-Beep conditions at Cz. Although we did not find significant developmental effect, we observed a clear early-late RP in all age groups in Action-Beep condition.* **B.** *Topography maps for early and late RP for each group in Action-Beep condition.*

Table 4.2 *Mean early-late readiness potential in Beep-Only and Action-Beep conditions for each age-groups. Standard errors of the mean presented in the brackets.*

	Mid-Adolescents		**Late-Adolescents**		**Adults**	
	Beep-Only	**Action-Beep**	**Beep-Only**	**Action-Beep**	**Beep-Only**	**Action-Beep**
Early RP	-0.48 (.40)	-1.75 (.51)	-0.43 (.37)	-0.96 (.47)	-0.01 (.38)	-0.96 (.48)
Late RP	-0.79 (.33)	-2.81 (.62)	-0.27 (.30)	-1.82 (.58)	0.22 (.31)	-2.22 (.59)

4.5.2.4 Correlational Analysis

4.5.2.4.1 The Relationship between Outcome Binding and Sensory Attenuation

Outcome binding and sensory attenuation are considered to be generated by the same mechanisms (Waszak et al., 2012). To test if this was the case, we examined correlations between these two measures. We first separately averaged N1 and P2 attenuation scores in each age group in left (FC3, C3 and CP3), central (FCz, Cz and CPz) and right (FC4, C4 and CP4) electrodes to reduce the number of correlations performed. We found a significant positive correlation between outcome binding and P2 attenuation on the right-side electrodes only in our mid-adolescent group ($r = 0.591$, $p = 0.006$, $N = 20$) (Figure 4.6A). However, this correlation was not significant in late-adolescents ($r = 0.36$, $p = 0.12$, $N = 20$) or in adults ($r = 0.19$, $p = 0.4$, $N = 20$). All other correlations between outcome binding and N1 or P2 attenuation in late-adolescent and adult groups were not significant ($p > 0.05$, Table 4.3).

Table 4.3 *Correlations of outcome binding with N1 and P2 attenuation at each age-group.*

		Outcome Binding			
		Mid-Adolescents	**Late-Adolescents**	**Adults**	**Overall**
Left Side	**N1 Attenuation**	r = 0.11 p = .63 n = 20	r = -0.41 p = .07 n = 20	r = 0.05 p = .82 n = 20	r = -0.06 p = .61 n = 60
	P2 Attenuation	r = -0.26 p = .26 n = 20	r = 0.13 p = .57 n = 20	r = -0.31 p = .17 n = 20	r = 0.001 p = .99 n = 60
Central	**N1 Attenuation**	r = 0.15 p = .52 n = 20	r = 0.09 p = .70 n = 20	r = -0.03 p = .89 n = 20	r = 0.08 p = .52 n = 60
	P2 Attenuation	r = 0.11 p = .63 n = 20	r = 0.07 p = .75 n = 20	r = -0.27 p = .24 n = 20	r = 0.09 p = .49 n = 60
Right Side	**N1 Attenuation**	r = -0.30 p = .19 n = 20	r = -0.10 p = .66 n = 20	r = -0.26 p = .26 n = 20	r = -0.09 p = .47 n = 60
	P2 Attenuation	**r = 0.59** **p = .006 *** **n = 20**	r = 0.36 p = .12 n = 20	r = 0.19 p = .40 n = 20	**r = 0.42** **p = .001** ***** **n = 60**

Note: *Significant correlations presented in bold. Left side electrodes: FC3, C3, CP3; Central electrodes: FCz, Cz, CPz; Right side Electrodes: FC4, C4 and CP4*

4.5.2.4.2 The Relationship between Outcome Binding and Readiness Potential

We next investigated the relationship between both early and late readiness potential and outcome binding (Table 4.4). A significant positive correlation between outcome binding and late readiness potential was found only in the mid-adolescent group (r = 0.60, p = 0.014, N=16). Since the late readiness potential values were negative, this relationship was the opposite. That is greater negativity was associated with smaller outcome binding (Figure 4.6B). To check that this relationship was not due to the relatively high late readiness potential values in some participants (see Figure 4.6B), we also conducted a Spearman's rank-order correlation. Similarly, it also revealed a significant correlation between late readiness potential and outcome binding in mid-adolescents (r_S = 0.71, p = 0.002, N = 16), and no significant correlation between outcome binding and readiness potential (early and late) in other age-groups (p > 0.05).

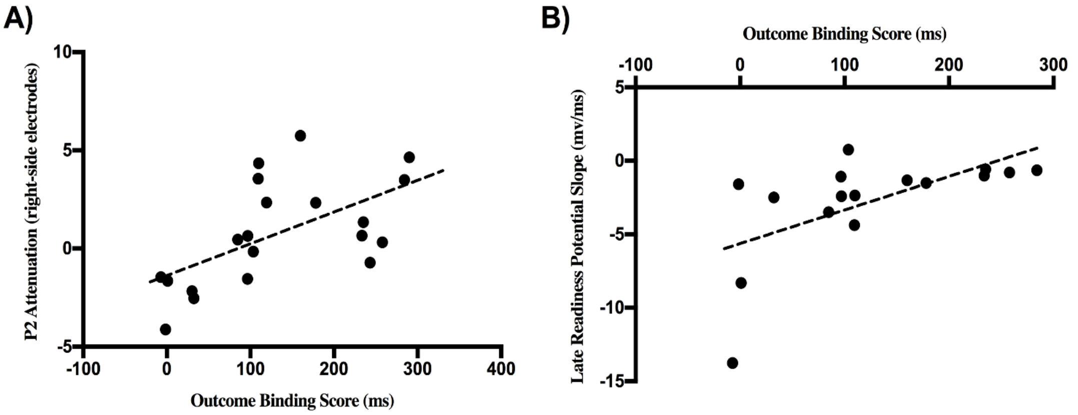

Figure 4.6. A) *Greater P2 attenuation in the right-side electrodes was associated with greater outcome binding scores in mid-adolescents.* **B)** *Greater negativity in the late readiness potential was associated with smaller outcome binding in mid-adolescents.*

Table 4.4. Correlations of outcome binding with early and late readiness potential

	Outcome Binding			
	Mid-Adolescents	**Late-Adolescents**	**Adults**	**Overall**
Early Readiness Potential	r = 0.32 p = .21 n = 16	r = -0.25 p = .27 n = 20	r = -0.24 p = .30 n = 19	r = 0.003 p = .98 n = 55
Late Readiness Potential	**r = 0.60** **p = .01** * **n = 16**	r = -0.07 p = .76 n = 20	r = -0.28 p = .24 n = 19	r = 0.19 p = .16 n = 55

4.6 Discussion

This study examined developmental changes in implicit sense of agency (SoA) using intentional binding phenomenon and its neural correlates during the transition from adolescence to adulthood. We found greater outcome binding scores in mid-adolescents compared to adults where we observed a trend level decreasing outcome binding from mid-adolescence through late-adolescence to adulthood. That is, we found that perceived temporal linkage of outcome towards action was greater in mid-adolescents compared to their adult counterparts. Our ERP data that were time-locked to auditory stimulus (self-triggered vs. computer-triggered sound) revealed greater P2 attenuation for the self-triggered sound in mid-adolescents compared to the older age-groups. However, neither N1 attenuation nor the readiness potential (from EEG data time-locked to the action) was associated with any significant age effects. Interestingly, in mid-adolescents only, greater outcome binding scores were significantly associated with greater P2 attenuation and smaller negativity in the late RP. Overall, this pattern of results suggests that mid-adolescents have a greater experience of implicit agency, which may be mediated by a specific neural process that acts to over-attenuate their action outcomes. The results from this study highlight that the transition from adolescence into adulthood is a critical period for the development of SoA.

Our finding that mid-adolescents (13-14 years old) have greater outcome binding compared to adults (25-28 years old) with a linear decreasing developmental trend from mid-adolescence through late-adolescence to adulthood suggests that mid-adolescents experience greater implicit agency for their action outcomes. This was similar to our previous findings where we observed a steady decrease from childhood (9-10 years old) to late-adolescence (18-20 years old) with mid-adolescents being in between. However, critically our findings were different for adults in these two experiments. In the previous experiment (Chapter 3), outcome binding increased from late-adolescence to adulthood, whereas in the present experiment it decreased from late-adolescence to adulthood. It is possible that this is due to differences in the temporal contiguity of actions and the outcomes in the two studies. In the previous experiment, we used 250 ms delay duration between actions and outcomes whereas in the current experiment we used 450 ms delay duration to avoid motor contamination on the auditory ERPs. Temporal contiguity has been shown to be an important factor for intentional binding measured in adults (discussed in detail in section 1.3.1). That is increasing delay decreases the intentional binding effect in adults (Buehner, 2012; Cravo et al., 2011; Haggard et al., 2002). However, the effects of temporal contiguity on intentional binding is unknown in younger age groups and it might be smaller. Intentional binding can be considered as the effect of voluntary action on the perceived temporal relationship of actions and outcomes and this effect might be operating better for short intervals as discussed in section 1.3.1. Adults might be better at differentiating the decreasing relationship with the increasing delay compared to younger age groups causing a reduction in intentional binding. Therefore, it is possible that, in adults, the perceived temporal linkage between actions and outcomes are reduced for longer delay durations due to the contiguity effect whereas in shorter delay durations this linkage is stronger; however, this contiguity effect might be to a lesser degree for younger age groups. Therefore, this might be the reason why we found differential developmental trajectories for intentional binding for short and long delay durations. This idea should be further investigated in the future studies to be able to understand the differential developmental trajectory for different delay durations. Nonetheless, this current study suggests a greater implicit agency experience for long (450 ms) delay durations during mid-adolescence.

Adolescence is an important period when the brain undergoes significant final maturational remodelling processes (Asato et al., 2010; Gogtay et al., 2004; Luna et al., 2010; Sowell et al., 2003). It is possible that the maturation of SoA related brain regions such as parietal regions (angular gyrus) and frontal regions (DLPFC and pre-SMA/SMA) or their improving connectivity with age (Gogtay et al., 2004; Sowell et al., 1999) might cause the decreasing developmental trajectory we observed in outcome binding. For instance, it was shown that stimulating the angular gyrus using tDCS decreased outcome binding effect (Khalighinejad & Haggard, 2015). Similar decreasing effect might be observed developmentally because of increasing top-down influence from frontal areas to the angular gyrus activity with age. That is, better top-down modulations of the angular gyrus activity together with the maturation of frontal areas might be associated with the decreasing outcome binding effect we observed from mid-adolescence to adulthood.

In terms of neural mechanisms underlying increased outcome binding observed in mid-adolescents, we found that mid-adolescents showed greater P2 attenuation when the beep they heard was caused by their own action (button press) compared to late-adolescents and adults. In contrast, we did not observe a developmental effect on N1 attenuation. Accordingly, it was also previously found that there is a relationship between explicit judgements of agency and P2 but not N1 attenuation in adults (Timm et al., 2016). Furthermore, we also found a significant relationship between outcome binding and P2 attenuation specifically in mid-adolescents, such that greater outcome binding scores were associated with greater P2 attenuation in mid-adolescents. However, it should be noted here that this relationship was found in the right-side electrodes, but the developmental effects we observed were found in the left-side and central electrodes. This may suggest that correlation of P2 attenuation with outcome binding and developmental effects might be related to differential processes. This relationship might also be a type one error due to running high number of correlations. Although we tried to reduce this possibility by using Benjamini-Hochberg correction, this finding should be replicated in the future studies. Furthermore, our findings suggest a distinctive developmental trajectory for N1 and P2 attenuation. Our finding that P2 attenuation did not significantly differ between late-adolescents and adults suggests that it becomes adult-like during late-adolescence, whereas N1 attenuation was already adult-like from mid-adolescence. This late maturation of the P2 attenuation might be beneficial in terms of learning and refining agency related processes before adulthood as P2 found to be a long-lasting correlate of auditory perceptual learning and this learning effect found to decrease from adulthood to old age (Ross & Tremblay, 2009).

It has been suggested that sensory attenuation is a result of an outcome prediction process that stems from motor preparation (i.e. efferent copy) (Blakemore et al., 2000; Waszak et al., 2012) which acts to predict what would be the outcome of our actions before they reached to the sensory cortex, so that sensory outcomes produced by ourselves are attenuated (or less salient). The differential developmental effect on N1 and P2 attenuation can be explained by differences in the time course of the development of lower- and higher-level predictive processes. Notably, there has been increasing evidence that N1 attenuation might be representative of the orienting lower-level predictions for the outcomes, whereas P2 attenuation might be representative of the higher-level sensory specific predictions for the outcomes (Cao et al., 2017; Hughes, 2015; Hughes & Waszak, 2014; Sanmiguel et al., 2013). That is, N1 attenuation might be a process which helps the system to know something is going to occur as a consequence of the action, whereas P2 attenuation might be a process that aids the system to know specifications of this consequence. Hence, it is possible that the differential developmental effect we observed in this study regarding the N1 and P2 attenuation can be explained by potential age-dependent differences in the development of lower- and higher-level predictive processes. We suggest that lower-level prediction processes may already mature before mid-adolescence as reflected in similar levels of N1 attenuation in all of our three age groups, whereas higher-level prediction processes might still be maturing during mid-adolescence and only become adult-like in late-adolescence.

The developmental effect we found on P2 attenuation was only observed on the central and left side electrodes, which were contralateral to the action hand since our participants performed the button presses always with their dominant right hand. This lateralised developmental effect on the size of P2 attenuation to the self-generated auditory stimulus may suggest an involvement of the motor prediction processes in this effect. In addition, this lateralised effect suggests that these differences are not a result of age-related differences in attentional processes. Since, if that was the case, one would expect to see similar effects in both right and left hemispheres (Griffin, Miniussi, & Nobre, 2002). Also, one would expect to see developmental differences on N1 attenuation because N1 has been shown to be sensitive to attention (Tomé, Barbosa, Nowak, & Marques-Teixeira, 2015). However, we did not observe such an effect. In addition, it is unlikely that this developmental effect was the result of potential motor contamination caused by the button press on the P2 amplitude. As, first, in order to minimise the motor contamination on N1 and P2 from preceding motor response, a delay of 450 ms between button press and auditory stimulus was used in this study based on previous studies (Hughes et al., 2013a; Hughes & Waszak, 2011; Poonian et al., 2015). Second, if this developmental difference on P2 attenuation was caused by motor contamination, similar results should have been observed for N1 attenuation since it occurs even closer to the time of the button press compared to P2 and would therefore have been affected by motor contamination more, which was not the case. Although we found reliable N1 attenuation in all age-groups, we found no developmental differences in the degree of this attenuation. Hence, we suggest that the most parsimonious explanation for our developmental P2 attenuation results is that it is related to the outcome prediction processes associated with the voluntary action preparation.

We initially predicted the involvement of the predictive processes in both outcome binding and sensory attenuation to gradually increase with age. This was based on the late maturation of the pre-frontal/frontal areas (DLPFC, Pre-SMA, SMA) that are suggested to be involved in these processes (Khalighinejad et al., 2016; Moore et al., 2010). Hence, we expected an improvement in predictions of action outcomes with age. Consequently, better predictions, as suggested by pre-activation account (Hughes et al., 2013b; Roussel et al., 2013; Waszak et al., 2012) and comparator model (Blakemore et al., 2000), would result in greater sensory attenuation with age. However, we found the opposite; both outcome binding and P2 attenuation decreased with age from mid-adolescence to adulthood, becoming adult-like in late-adolescence. One possible explanation for this discrepancy is that mid-adolescents might be relying on predictive processes more in this delay duration than older participants for constructing their experiences of agency. Adults might be using a different strategy when constructing their agency for this delay duration (e.g., retrospective, inference based) compared to mid-adolescents. This idea is supported by our finding that only mid-adolescents showed significant correlations between their outcome binding scores and their late RP and P2 attenuation scores.

In terms of RP, we did not observe significant age dependent changes in the early or late parts of RP. We only found a negative correlation between late RP and outcome binding in mid-adolescents. This may suggest that although RP amplitudes did not differ across age groups it has a differential relationship with outcome binding across age groups. That is, we did not find a compensatory over-recruitment of motor preparation processes since we did not find a significantly different RP between our three different age groups, rather we only found mid-adolescent specific correlations which might reflect a compensatory over-reliance on the motor preparation instead. It was found in a previous study conducted with adults that early RP, which has been suggested to originate from pre-SMA, was correlated with outcome binding (Jo et al., 2014). However, we did not observe such significant correlation of outcome binding with the early RP in all age groups or late RP in late-adolescents and adults. This might be due to the increased delay duration between action and the outcome in the current study (current study: 450 ms, Jo et al., 2014: 250 ms) which might be causing participants to engage retrospective processes more instead of predictive processes as discussed previously. This might have consequently reduced the relationship between early RP and outcome binding. Therefore, developmental effects on the involvement of RP in outcome binding should be further investigated using both short and long delay durations in the future studies as it might also reveal the involvement of predictive processes in the short and long action outcome temporal relationships.

Our overall findings suggest that developmental changes observed in implicit SoA as measured by outcome binding and sensory attenuation (specifically P2 attenuation) persist into adolescence and become adult-like during late-adolescence. Our findings can have implications for understanding neural basis of SoA as it shows that there is a developmental trajectory for both outcome binding and sensory attenuation. Future studies using similar design with imaging techniques can be useful to understand the neural basis of SoA. Our findings can also have implications for understanding agency related neurodevelopmental disorders such as schizophrenia (Frith et al., 2000; Synofzik et al., 2010; Voss et al., 2010) which mostly emerges during the transition from adolescence to adulthood (Gomes et al., 2017; Harrop & Trower, 2001). It has been previously reported that schizophrenia patients show exaggerated retrospective binding (inference based) with a specific impairment in predicting action outcomes (Voss et al., 2010) as well as a lack of sensory attenuation effect (Blakemore, Smith, Johnstone, & Frith, 2000). This specific impairment of outcome prediction might be caused by possible abnormal developmental changes in this process. Finally, our finding that implicit agency experience reaches adult-like form during late-adolescence can have implications for criminal responsibility in the legal systems for which SoA has been suggested to be a key factor (Chris D. Frith, 2014; Haggard & Tsakiris, 2009; Moretto et al., 2011). However, the effect of temporal contiguity should be investigated further since we found a differential developmental trajectory for short (250 ms) and long (450 ms) delay durations.

4.7 Study limitations

Results from the current study need to be considered in light of the study limitations. Firstly, this study only focused on outcome binding, not action binding which is the perceived temporal shift of action towards outcome. The reason we decided to focus on outcome binding developmentally was that we first wanted to focus on measures that are associated with top-down predictive processes in frontal brain regions (Haggard, 2017; Khalighinejad & Haggard, 2015a; Moore et al., 2010; Summerfield et al., 2018; Waszak et al., 2012), which might show protracted development throughout adolescence. Hence, our results might not be generalised for action binding which might rely on different processes and future studies might be useful to investigate its development during adolescence. Second, it was previously shown that 250 ms delay between participants' button presses and the auditory feedback produces maximum intentional binding effect (Haggard et al., 2002). However, we inserted 450 ms delay between a button press and an auditory feedback. This delay time might have reduced the developmental effect we found, because 250 ms delay time might produce stronger effect. Nevertheless, we used 450 ms delay for minimising the possible influence of motor-related brain activity on auditory ERPs. Hence, future studies might want to use both 250 ms and 450 ms to investigate the developmental effects on different delay times. In such future studies action only condition may be included to account for motor contamination on ERPs (e.g. Baess et al., 2008). Furthermore, future studies should also include a child group to investigate the full developmental trajectory (see Casey, 2015) of implicit SoA within short and long delay durations.

In addition, seminal early intentional binding and sensory attenuation studies also included a passive condition where participants' passive actions (e.g.: transcranial magnetic stimulation triggered action) generated the outcome (Haggard et al., 2002) or where participants passively listened to a playback of the beep they triggered previously (Schafer & Marcus, 1973). These conditions were included in these studies to show that intentional binding and sensory attenuation effects were specific to voluntary action condition but not to the passive condition. However, in the current study we did not include such a condition since the main aim of the current study was to investigate the effect of development, which was included as between subject variable, on these phenomena instead of assessing the existence of them which has been demonstrated in the previous studies (Moore & Obhi, 2012; Waszak et al., 2012). Although there might also be age effects in the passive action condition, the lack of such a significant effect was shown previously (Cavazzana et al., 2014).

4.8 Conclusions

The current study, for the first time, demonstrated that mid-adolescents show greater implicit sense of agency as indexed by outcome binding and concurrent attenuation of the auditory P2, which became adult-like in late-adolescence. We suggest that processes underlying implicit SoA might be operating differently, such as over-reliance on predictive processes, in mid-adolescence compared to late-adolescence and adulthood. Our study suggests that future studies of intentional binding should not only focus on N1 (associated with lower-level outcome prediction) but also P2 attenuation (associated with higher-level outcome prediction) which may show a protracted development. We suggest that these findings can have implications for the future research aiming to understand neural basis of SoA and outcome prediction impairments in schizophrenia which might be related to abnormal development of this process.

Chapter 5

5. General Discussion

Everyday voluntary actions are accompanied by an intrinsic feeling that we are in control of our actions and their outcomes (Gallagher, 2000; Haggard, 2017; Pacherie, 2008). The current thesis aimed to investigate the neural basis of this feeling of agency by focusing on the perceived temporal relationship between voluntary actions and their outcomes. The importance of action and outcome temporal relations comes from its role on affecting perceived agency and being affected by agency. As discussed in Chapter 1, action outcome temporal relations can affect causality and SoA (Blakemore et al., 1999; Dickinson, 2001; Haggard et al., 2002; Shanks et al., 1989; Walsh & Haggard, 2013); likewise, causality and SoA can affect action outcome temporal relations as seen in sensorimotor temporal recalibration and intentional binding (section 1.1) (Cravo et al., 2009; Haggard et al., 2002; Stetson et al., 2006; Timm et al., 2014). Therefore, this thesis focused on these two phenomena that are closely tied to SoA to investigate the neural basis of SoA using transcranial direct current stimulation, developmental approach and electroencephalogram (EEG). The results from the empirical studies add to the current knowledge by showing the sensory cortical involvement in temporal recalibration (Chapter 2), the developmental trajectory of intentional binding from childhood to adulthood as measured by two different methods (Chapter 3) and neural correlates of intentional binding during the transition from adolescence to adulthood (Chapter 4). This chapter will first summarise the main findings from the empirical work undertaken in this thesis. Then, it will discuss the possible implications of these findings for understanding SoA in health and disease as well as for understanding adolescence. It will be followed by the strengths and limitations of this work. Finally, based on the findings, future directions will be discussed and general conclusions will be drawn.

5.1 Summary of and Conclusions from Key Findings

First part of the empirical work in this thesis (Chapter 2) investigated the involvement of sensory specific brain areas (auditory and visual cortices) in sensorimotor (visual-motor and audio-motor) temporal recalibration. Temporal recalibration is an important phenomenon for SoA especially in situations when actions and outcomes are separated in time (see Walsh & Haggard, 2013 for the effect of temporal recalibration on intentional binding). However, brain mechanisms regulating temporal recalibration have not been well understood. There were studies suggesting a supramodal mechanism (a central mechanism beyond the sensory specific brain areas) (Heron et al., 2009) that regulates temporal recalibration or motor shift that is providing transference of temporal recalibration between modalities (Sugano et al., 2010) (see section 1.2). However, there were findings that were contradicting with these accounts (e.g., asymmetric transference of temporal recalibration between modalities) suggesting sensory specific brain areas might be at play (Sugano et al., 2012). However, the involvement of the modality specific brain areas in sensorimotor temporal recalibration has been unknown since it has not been directly tested using brain stimulation. Hence, Chapter 2 investigated this issue by stimulating auditory and visual cortices using cathodal tDCS.

Chapter 2 showed, for the first time, that temporal recalibration, a delay compensation process that is important for causality as well as SoA, can be modulated by a non-invasive brain stimulation technique. Furthermore, findings from this work provided direct evidence for the involvement of visual cortex in the visual temporal recalibration process together with possible, albeit weak, modulatory influence of the auditory cortex. These results suggested that sensory specific brain areas are at play during visual temporal recalibration instead of a central mechanism (Heron et al., 2009) or motor component shift (Sugano et al., 2010) as proposed previously. Furthermore, both auditory and visual cortex stimulation did not have any significant effect on auditory temporal recalibration suggesting the robustness of the auditory temporal processing (Andreassi & Greco, 1975; Molholm et al., 2002; Stone et al., 2001).

The second and third (Chapter 3 and 4) parts of the empirical work presented in this thesis took developmental approach on board based on the literature suggesting maturational changes in the SoA related brain areas which consequently indicates a developmental trajectory for SoA (discussed in section 1.6). These maturational changes might cause differences in the agency experience and its underlying processes which could consequently provide a window for understanding the neural basis of SoA.

Therefore, developmental approach for understanding possible changes in SoA and their neural basis would be fruitful. Instead of temporal recalibration, intentional binding, which is a similar phenomenon and has been considered as an implicit measure of SoA (Haggard, 2017; Moore & Obhi, 2012) was used since it could better reflect the developmental effects on SoA compared to temporal recalibration which focuses on the delay adaptation process.

Although neural circuits that are associated with different aspects of SoA (Pre-frontal, frontal and parietal areas linked with action selection, action preparation and outcome monitoring) goes through maturational processes from childhood through adolescence to adulthood (Gogtay et al., 2004; Luna et al., 2001; Sowell et al., 1999), there has been no studies investigating SoA during this period (discussed in section 1.6). Therefore, Chapter 3 examined the developmental trajectory of SoA as indexed by intentional binding from childhood to adulthood using two different tasks (Libet Clock and Stream of Letters). This chapter provided an overview of how overall intentional binding as well as action and outcome binding changes throughout childhood (9-10), mid-adolescent (13-14), late-adolescent (18-20) and adult period (25-28). Furthermore, Chapter 3 was able to provide comparisons between two different measurement methods of intentional binding in terms of the binding they measure, developmental trajectory they capture and their suitability for using in developmental studies.

Using intentional binding as an implicit measure of SoA, Chapter 3 showed, for the first time, that adolescence may be an important period for the development of SoA (when intentional binding was measured by Libet Clock method). Interestingly, findings from this work revealed a U-Shaped developmental trajectory for the SoA, where intentional binding was greatest in childhood and decreased throughout mid-adolescence until late-adolescence where it was the lowest and increased to about childhood level in adulthood (See Figure 3.2A). The type of developmental trajectory captured by the Libet Clock method revealed a late-adolescent specific developmental change in SoA. This suggested that late-adolescence might be an important period for the development of SoA. Interestingly, after a decrease of intentional binding from childhood to late-adolescence, adults displayed an increase in intentional binding which reached to about childhood levels. As discussed in Chapter 3, this developmental trajectory might reflect a developmental shift from relying on retrospective process (external cues) in childhood to predictive processes (internal cues) in adulthood with a balance in late-adolescence. This developmental shift could be underlined by the prolonged maturation of the brain areas regulating predictive processes (discussed further in section 3.5). Furthermore, the developmental trajectory of overall intentional binding was mainly driven by outcome binding whereas action binding was similar across age groups suggesting earlier development of the processes underlying action binding.

Chapter 3 also revealed that Libet Clock and Stream of Letters, two tasks that have been used for measuring intentional binding differ in terms of the developmental trajectory they suggest and also the intentional binding measured by these two tasks do not correlate. These results suggest these two tasks might be measuring different aspects and/or mechanisms of intentional binding. Therefore, overall, this chapter also suggests that intentional binding and its observed developmental profile might be susceptible to the features of the task used and these features should be considered when interpreting intentional binding results from different task methods (e.g. contextual predictability, temporal precision and difficulty of the method). There is also an intriguing question that stems from these findings. Can agency experience differ based on how it is measured even though agency levels are not manipulated? For instance, participants agency levels were not manipulated in this study but how their agency was measured changed and it revealed different levels of agency as indexed by intentional binding. Intentional binding's this susceptibility to task features observed here requires future investigation for understanding its relevance for being an implicit measure of agency since these two tasks revealed different levels of intentional binding that did not have a significant relationship with one another even though participants agency levels were not manipulated.

Based on the findings in Chapter 3, Chapter 4 examined the neural correlates of the developmental trajectory found in Chapter 3 by examining the ERPs that have been associated with SoA. These were ERPs that have been shown to be involved in voluntary action preparation - the readiness potential (Haggard & Eimer, 1999; Jo et al., 2014; Libet et al., 1983) and outcome processing, as measured by the attenuation of N1 and P2 ERPs (Aliu et al., 2009; Baess et al., 2008; Hughes et al., 2013a; Schafer & Marcus, 1973). These ERP components were investigated since voluntary action and outcome processes are central to SoA and these components have been associated with SoA. For instance, it was found that increased early readiness potential was associated with increased outcome binding (Jo et al., 2014), and self-generated stimulus resulted in attenuated neural response (N1 and P2) compared to externally generated one (Schafer & Marcus, 1973). Libet Clock method was used in this study since it showed smaller variability in participants' judgement errors and participants also found it easier compared to Stream of Letters method (Chapter 3).

Chapter 4 revealed the developmental trajectory of SoA at both behavioural and neural levels. It specifically showed how outcome binding changes from mid-adolescence to adulthood and what are the neural associates of this change. Behavioural data showed that mid-adolescents had greater outcome binding, perceived temporal linkage of outcomes to actions, compared to adults with late-adolescents being in the middle where we observed a trend level main effect of age on outcome binding. Similarly, ERP results revealed that P2 attenuation is greatest in mid-adolescents and decreases with age, where mid-adolescents had significantly greater P2 attenuation for the self-generated stimulus (outcome) than the older participants. In contrast, neither N1 nor readiness potential showed any developmental effects. Interestingly, in the mid-adolescent group only, greater outcome binding scores were associated with greater P2 attenuation and smaller negativity in the late readiness potential. These findings suggested a greater experience of implicit agency, which may be mediated by a neural over-attenuation of action outcomes and over-reliance on motor preparation in mid-adolescents, which we found to become adult-like in the late-adolescence.

5.2 Implications for Understanding the Development of Sense of Agency

Developmental aspects of implicit and explicit agency during adolescence have been largely neglected. This is surprising considering the maturational changes occurring in the SoA related brain areas throughout adolescence (see section 1.6.1). The empirical work undertaken in this thesis showed that adolescence can be a critical period for the development of implicit agency (Chapter 3 and 4). This work establishes the basis for future studies that aims to address some important issues for understanding implicit agency indexed by intentional binding and its functional significance at different developmental stages. For instance, the mere evidence that intentional binding, which has been suggested to reflect SoA, changes throughout development is interesting per se. That is because it suggests that we might not have a default experience of agency that is stable throughout development but instead it might be changing and developing throughout developmental stages. There are still unanswered important questions. For instance, we do not know the functional significance of this developmental change over time or how it would affect some adolescent specific behaviours (e.g increased risk-taking Steinberg, 2008). This might also have functional effects on children's learning of action outcome associations due to their greater perceived temporal linkage between actions and outcomes. Hence, investigating functional significance of changing SoA from childhood to adulthood further is important.

In addition, the empirical studies presented in this thesis have some methodological implications for the future developmental studies. First, this thesis provided a comparison (Chapter 3) between two measurement methods of intentional binding during childhood, adolescence and adulthood. It suggested that Libet Clock method was less variable and reported to be easier compared to Stream of Letters suggesting Libet Clock method might be more preferable in the developmental studies that has an age range from 9 to 28 years old. Second, this thesis showed that Libet Clock method can be used to measure intentional binding together with sensory attenuation (measured with ERPs) and it provides behavioural support for the neural data (Chapter 4). This approach can be implicated in the future developmental studies aiming to understand neurodevelopment of implicit agency. The studies presented in this thesis establishes the basis for such future studies.

5.3 Implications for Understanding Neural Basis of Sense of Agency

As discussed in the general introduction (section 1.5), Chapter 3 and Chapter 4, higher order areas, specifically fronto-parietal circuits including DLPFC, Pre-SMA, SMA and angular gyrus has been investigated for their role in implicit agency, especially by non-invasive brain stimulation studies that can provide a causal link between the area and its involvement in the process (Cavazzana et al., 2015; Hughes

2018; Khalighinejad & Haggard 2015; Khalighinejad et al., 2016; Moore et al., 2010). However, involvement of the sensory specific brain areas (e.g. auditory and visual cortices) have been largely neglected so far. To my knowledge, for instance, there have been no brain stimulation studies investigating the role of the visual cortex and only one investigating the role of the auditory cortex in implicit agency. This is surprising, especially considering auditory cortex, since most of the studies investigating implicit agency have used auditory stimulus as the outcome of the actions (see Moore & Obhi, 2012 for a review). However, these brain regions can be an important part of the SoA process as they form the early processing of the outcomes.

With a different approach to the implicit agency studies using intentional binding, Chapter 2 investigated the role of both auditory and visual cortices in action outcome temporal relationship using temporal recalibration phenomenon. Temporal recalibration is a delay compensation process that is important for agency experience especially for the delayed outcomes of our actions by bringing them closer in time (Stetson et al., 2006; Timm et al., 2014). Chapter 2, using tDCS, showed a direct evidence for the involvement of the visual cortex in the visual temporal recalibration process together with a possible weak modulatory effect of auditory cortex. However, there was no detectable effect of both auditory and visual cortex stimulation on auditory temporal recalibration. These finding suggested that sensory specific cortical regions might be at play when our brain is trying to regulate the temporal link between our actions and their outcomes. This study, furthermore, suggested a differential nature of the underlying mechanisms for action outcome temporal relationships in visual and auditory modalities. This could be important for understanding the neural basis of agency experience in different modalities or mixed modalities since modality specific features of agency experiences has been mostly neglected so far as discussed above (e.g. action can lead to an outcome that include both visual and auditory information). For instance, SoA can have different mechanisms for auditory and visual outcomes of our actions as indicated in this study. The involvement of lower-level brain areas in SoA can be investigated using a non-invasive brain stimulation technique as in this study together with implicit and explicit measures of SoA. Investigating modality dependent nature of the action outcome temporal processing and its possible effects on agency experience can be useful for understanding the contribution of the lower level areas into our agentic experiences in different modalities.

Higher order areas have driven more attention for pinpointing the neural basis of SoA. Both brain stimulation and neuroimaging studies highlighted a fronto-parietal network that is involved in SoA process (discussed in section 1.5). It was previously suggested in a recent review that SoA may emerge from predictive and retrospective interplays between pre-fontal/frontal areas that are involved in action selection, planning and initiation, and parietal regions that are involved in monitoring of these and their outcomes (Haggard, 2017). In line with this, the idea of a balanced and context dependent combination of the predictive and retrospective components might be key factor for a reliable SoA has been suggested based on the cue integration approach (Chambon et al., 2014; Moore & Haggard, 2008; Moore & Fletcher, 2012; Synofzik et al., 2013). The fronto-parietal network associated with SoA undergoes critical final maturation processes from childhood to adulthood (discussed in section 1.6) which consequently can lead to developmental differences in agency experience. Therefore, this thesis, in Chapter 3 and 4, investigated the developmental trajectory of SoA and its neural correlates from childhood throughout adolescence to adulthood.

Findings from Chapter 3 showed a U-shaped developmental trajectory of SoA (as measured by intentional binding with the Libet Clock method) from childhood to adulthood where it was lowest in late-adolescence. This developmental trajectory is difficult to explain with a linear maturation of SoA related brain regions. It is possible that this trajectory may be caused by a developmental shift from relying on retrospective to predictive components of agency from childhood to adulthood with a balance in late-adolescence based on the prolonged maturation of the frontal areas that are associated with the predictive processes (discussed in section 3.5). This suggests a linearly increasing involvement of the predictive processes in SoA as well as linearly decreasing involvement of the retrospective processes in SoA with the maturation of the frontal regions. In childhood, children might be relying on retrospective processes which might be mediated by earlier developing parietal areas (Sowell et al., 1999) involved in action and outcome monitoring (Farrer et al., 2004; Farrer et al., 2008; Khalighinejad and Haggard, 2015; Voss et al., 2017). It should be noted here that this type of developmental trajectory would only be observed in predictable contexts since in unpredictable situations older participants have also been shown to use retrospective processes when constructing the experience of agency (Moore & Haggard, 2008). In summary, we have argued for a developmental shift of the agency cues used when constructing agency experience based on the maturation of the frontal brain regions which consequently would increase the reliability of the predictive processes. This idea is in line with the cue integration approach which suggests agency cues are weighted based on their reliability to construct a dependable SoA (Moore & Fletcher, 2012; Synofzik et al., 2013). This chapter also suggested that the adolescent period, specifically late-adolescence might be a critical period for SoA as measured with intentional binding.

Building on Chapter 3, Chapter 4 investigated the developmental changes in the SoA as measured with outcome binding and its neural correlates in the transition from adolescence to adulthood. Our findings, which showed a linearly decreasing trend of outcome binding where we observed greater temporal linkage of outcomes towards actions (outcome binding) in mid-adolescents compared to adults, suggest a greater implicit agency in mid-adolescents. The developmental trajectory observed in Chapter 3 (U-shaped) and Chapter 4 (linearly decreasing) was in line with each other up to the late-adolescence period until where we observe a decrease in binding. However, they differ for the adult period where we observe an increase in Chapter 3 and a continuing decrease in Chapter 4 from late-adolescence to adulthood. We suggested that this difference might be a result of the adults' different strategies for high (250 ms delay) and low (450 ms delay) temporal contiguities compared to younger age groups which should be tested in future studies (discussed in section 4.6).

In terms of the neural mechanism of increased implicit agency observed in mid-adolescence, we found that mid-adolescents showed greatest attenuation of P2 when the beep they heard was caused by their actions. This P2 attenuation showed a linearly decreasing developmental trajectory from mid-adolescence to adulthood which was similar to the developmental trajectory observed for outcome binding suggesting that P2 attenuation might be the neural concomitant of implicit agency. However, there was no developmental effects on N1. In line with these findings, the relationship between explicit judgements of agency and P2 attenuation but not N1 attenuation was shown previously (Timm et al., 2016). Interestingly, we found a positive relationship between P2 attenuation and outcome binding specifically in mid-adolescents (discussed in section 4.6). That is greater attenuation of the neural response (P2) for self-generated stimulus was associated with greater temporal linkage of the self-generated stimulus towards action. This would be in line with the pre-activation account explanation of sensory attenuation and outcome binding. It suggests that greater pre-activations of the brain areas related to the processing of upcoming outcome would cause both greater sensory attenuation and greater outcome binding (Waszak et al., 2012).

The sensory attenuation phenomenon has been linked to outcome prediction processes (i.e. efferent copy, Blakemore et al., 1998; Blakemore et al., 2000; Waszak 2012) that can inform what would be the outcome of the actions before the actual outcome reached to the brain and sensory outcomes of actions are perceived less salient, i.e., attenuated (discussed in section 1.3.2). We suggested a developmental difference for the lower- and higher-level predictive processes to explain the differential developmental effects on N1 and P2 attenuation. Indeed, there has been increasing body of evidence suggesting that N1 attenuation might be representative of lower-level orienting predictions whereas P2 attenuation might be representative of higher-level sensory predictions of the outcome (Cao et al., 2017; Hughes, 2015; Hughes & Waszak 2014; Sanmiguel et al., 2013). Hence, N1 attenuation might be related to a process which helps the system to know, with rough predictions, that something is going to occur whereas P2 attenuation might be related to a process that helps the system to know the specifications of the outcomes. We suggested that lower-level prediction processes reflected with N1 attenuation might be already mature before mid-adolescence but higher-level predictive processes reflected in P2 attenuation is still maturing during mid-adolescence which becomes adult-like during late-adolescence.

Overall, Chapter 3 and Chapter 4 stressed that the transition from adolescence to adulthood can be a critical period for the development of SoA and its neural circuits. Chapter 3 suggested a U-shaped developmental trajectory of binding from childhood to adulthood where it was lowest in late-adolescence. We argued that this developmental trajectory might be driven by a developmental shift in the use of retrospective and predictive components when constructing agency from childhood to adulthood with a balance being reached in late-adolescence. This idea was based on the prolonged maturation of the frontal brain regions that are related to predictive processes. Chapter 4 suggested a linearly decreasing developmental trajectory of binding from mid-adolescence to adulthood (delay duration was increased from 250 ms in Chapter 3 to 450 ms in Chapter 4) where we also observed a linearly decreasing developmental trajectory for P2 attenuation. This study suggested P2 attenuation might be the neural concomitant of implicit agency and it also becomes adult-like during late-adolescence. The findings from Chapter 4 also suggested that processes of implicit SoA might be operating differently in different developmental groups such as an over-reliance to the predictive processes in mid-adolescence, possibly driven by still maturing frontal regions, compared to the older participants. This was also supported by the mid-adolescence specific correlation between outcome binding and late readiness potential. Our results across two studies suggest that developmental trajectory and underlying processes of SoA can possibly change depending on the temporal contiguity. Therefore, temporal contiguity should be considered in the future studies aiming to investigate the development of agency experience and its neural basis. Our results also suggest that future studies of implicit agency investigating neural basis of it should not only focus on N1 (associated with lower level predictions) but also P2 attenuation (associated with higher level predictions) which shows a protracted development.

Overall, the empirical work presented in this thesis contributed to our understanding of the neural basis of SoA by using a number of phenomena associated with SoA (temporal recalibration, intentional binding and sensory attenuation) and by employing a variety of techniques and approaches (tDCS, EEG and developmental approach). This thesis showed that developmental approach, especially focusing on adolescence period, can be useful for understanding the neural basis of SoA. The work presented in this thesis suggested that future studies should not only focus on N1 but also P2 attenuation together with behavioural measures (e.g. intentional binding measured with Libet Clock) as P2 attenuation might be the neural correlate of SoA. Findings of the current thesis also suggested that instead of focusing on only higher order areas, future studies should also investigate the possible modality specific roles of lower order areas in intentional binding and explicit agency such as sensory specific brain regions since it is possible that how our brain constructs the experience of agency might change depending on the modalities and their interaction. Our developmental approach can also be used in combination with behavioural measures (intentional binding) and brain imaging (e.g. fMRI) to further understand the brain areas of SoA and how development influences these areas and their potential role when constructing the agentic experiences. This thesis formed the basis of such future studies by showing the developmental effects on implicit agency and its neural correlates as well as by showing that Libet Clock method can be successfully employed in such studies.

5.3 Implications for Understanding Impaired Agency in Schizophrenia

Schizophrenia is a serious neurodevelopmental disorder which shows increased onset rates in the transition from adolescence to adulthood (late adolescence - young adulthood, Gomes et al., 2017 and Harrop & Tower, 2001). Impairments in SoA is one of the characteristics of the control delusions (e.g. an alien or something else is controlling my behaviours, or I can control people's behaviour) observed in individuals with schizophrenia, and it has been suggested to be associated with the impairments in action monitoring and predictive processes (Frith et al., 2000; Synofzik et al., 2010; Voss et al., 2010; Voss et al., 2017). For example, individuals with schizophrenia show a retrospective over-binding with a specific impairment in predictive processes (Voss et al., 2010). Furthermore, schizophrenia patients also exhibit a lack of sensory attenuation which has been shown to be driven by predictive operations in the brain (e.g. outcome prediction) (Blakemore et al., 2000).

The current thesis can have some implications for the future research aiming to understand the agency impairments in this neurodevelopmental disorder since, as mentioned above, adolescence is associated with a significant vulnerability in developing schizophrenia a disorder that involves distorted SoA. For instance, Chapter 4 showed that mid-adolescents show greater attenuation of the neural response to the outcomes of their actions (P2 attenuation) and greater temporal linkage of the outcomes towards their actions (Outcome binding) suggesting an increased implicit agency that is driven by predictive processes during mid-adolescence (13-14 years old) and it became adult-like in late-adolescence (18-20 years old). It is possible that specific impairments observed in the predictive components of SoA in schizophrenia might be associated with the abnormal neurodevelopmental changes in this predictive process during the transition from adolescence to adulthood.

Furthermore, findings from Chapter 2 might have therapeutic implications for schizophrenia patients exhibiting impaired SoA. That is, the decreasing effect of tDCS on temporal recalibration can have therapeutic implications for schizophrenia patients. It was shown that increased temporal recalibration can cause increased illusory temporal reversals of actions and outcomes (outcomes preceding actions which consequently violates causal order) which can diminish SoA (Timm et al., 2014). Also, it was shown that schizophrenia patients have exaggerated temporal compression between their action and outcomes through an intentional binding phenomenon which is a similar phenomenon to temporal recalibration. Therefore, reducing temporal recalibration effects might be useful for these patients and as shown in Chapter 2 tDCS can be used to reduce temporal recalibration effect.

5.4 Implications for Understanding Adolescent Behaviour

Adolescence is a prolonged developmental period that continues up to one's mid-twenties (Sawyer et al., 2018). It is associated with an increase in risk-taking behaviour which can result in harm to self and others, with a 200% increase in preventable deaths (accident, suicide, homicide) related to risk-taking (Casey et al., 2010; Paus, Keshavan, & Giedd, 2008). Adolescents are more likely to exhibit risky-behaviours compared to adults such as having unprotected sex, risky driving, binge drinking and drug use and misuse (Kim-Spoon et al., 2016; Steinberg, 2008; Victor & Hariri, 2016). There are a number of theories of adolescent risk-taking (Casey, 2015; Doremus-Fitzwater & Spear, 2016; Ernst, Pine, & Hardin, 2006; Shulman et al., 2016) However, a possible important underlying factor that could be associated with adolescent risky-behaviours has been neglected so far, sense of agency.

SoA forms the basis of feeling individual responsibility for our actions and their consequences; hence, it also forms the basis of societal and legal systems (Frith, 2014; Haggard & Tsakiris, 2009; Moretto et al., 2011). Our findings in Chapter 3 showed that late-adolescents might experience less implicit agency over the consequences of their actions in short delay (consequences close in time) durations compared to younger and older age groups. It is possible that the greatest reduction in SoA during late-adolescence might be a partial underlying factor for the increased risk-taking behaviour observed during late-adolescence (Steinberg 2008). This is because reduced SoA could be a factor of feeling less responsible for the consequences of their risky actions. However, there has been no studies investigating reduced SoA as being a possible underlying factor for increased risk taking during late-adolescence. It should be noted here that in contrast, in Chapter 4 we found an increased implicit agency experience in mid-adolescents for long delay durations (consequences distant in time) which may suggest proposed effects of agency on risk-taking might be modulated by the temporal contiguity of the actions and their consequences.

In addition to the implications for understanding adolescent behaviour, our finding that children show an increased temporal linkage between their action and its consequences (increased intentional binding) might be beneficial for children's learning action outcome causal relations. This is in line with the previous studies suggesting exaggerated explicit self-agency attributions in children (Metcalfe et al., 2010; Van elk et al., 2015). It was also shown previously that binding effect can be observed in as young as 4 years old children suggesting it is grounded in the causal learning early on (Blakey et al., 2018). They also showed that binding effect was not specific to the intentional action but it was a result of the causal relationship in long delay durations (900 - 1300 ms). Future studies might be useful to understand whether intentional action could make an additional boost over binding in shorter delay durations as influence of intentional action over binding might be operating in shorter delay durations since actions are usually followed by consequences with no or very short delays.

5.5 Strengths of This Work

One of the strengths of this thesis was its use of the tasks that focus on implicit measures (sensorimotor synchronisation, intentional binding and sensory attenuation) to examine agentic experiences. For example, sensorimotor synchronisation task, which is a tapping task in synchrony with a pacing stimulus (Sugano et al., 2012), was used to measure temporal recalibration effect instead of judgement based tasks (e.g. temporal order judgement task, Heron et al. 2009). In this study, we examined the involvement of the lower order areas (modality specific brain regions) in temporal recalibration process. However, the use of a temporal order judgement tasks might cause to an additional recruitment of higher order brain areas as well as causing to a possible response biases when making judgements (Sugano et al., 2010). Hence, using sensorimotor synchronisation task which requires simple motor actions (tapping) without making any judgements might have reduced these downsides of explicit judgement tasks. Furthermore, this thesis also used measures that have been widely employed as implicit measures of SoA, namely intentional binding and sensory attenuation (discussed in section 1.3). This approach helped this thesis to avoid/reduce possible downsides of explicit judgement tasks of SoA such as being vulnerable to demand characteristics, being open to metacognitive confounding factors (e.g. age differences in decision making), overestimation of self-agency (Haggard, 2017; Wolpe & Rowe, 2014) and being difficult to reliably obtain from patient groups (Wolpe & Rowe, 2014) or young age groups. Implicit measures that were used in this thesis avoid/reduce these factors by focusing on correlates of voluntary action processes that are sensitive to agency and infer agency based on these measures without asking anything about agentic experiences (Moore, 2016).

As another important strength, this work employed a variety of methods to examine SoA from different perspectives. These were tDCS, temporal recalibration, intentional binding measured with Libet Clock and Stream of Letters, developmental approach, EEG measures such as readiness potential, and N1 and P2 attenuation. For instance, Chapter 2 used a non-invasive brain stimulation technique (e.g. tDCS) which can provide direct evidence for the involvement of the area of interest in the task in hand by providing temporary impairments in these areas. Furthermore, examining intentional binding with both Libet Clock and Stream of Letters methods, which has not been investigated together before, provided evidence for intentional binding’s susceptibility to task characteristics. Additionally, instead of comparing two age groups (e.g. adolescent and adults), current thesis provided a wider perspective on the developmental effects on implicit agency by investigating age groups in childhood, mid-adolescence, late-adolescence and adulthood (e.g. U-shaped trajectory in Chapter 3 would not be captured without these wide range age-groups). Finally, one of the key strengths of the methods used in this thesis was the use of Libet Clock method together with N1 and P2 attenuation which provided a behavioural support for the EEG data. Libet Clock method was not considered in the previous sensory attenuation studies. To my knowledge only interval estimation tasks which do not let investigating action and outcome binding separately were used in the sensory attenuation studies (Pooninan et al., 2015). However, as suggested in the literature, it is possible that only the outcome binding might be associated with sensory attenuation and interval estimation methods would not enable measuring action and outcome binding (discuused in section 1.3 and 1.4). Hence, current thesis showed that Libet Clock can be successfully used in such studies and can provide further behavioural evidence as it did in this thesis. This study also, as a strength, showed that instead of focusing on one ERP component such as N1 attenuation, examining P2 attenuation as well as ERPs related to motor preparation such as readiness potential could be more fruitful (e.g. mid-adolescent specific positive correlations of outcome binding with P2 attenuation and late-readiness potential suggested a possible over-reliance on predictive processes in mid-adolescence). Therefore, the variety of the techniques, methods and perspectives used to examine SoA helped this thesis to contribute to our understanding of the development and the neural basis of SoA as well as providing a basis for the future neurodevelopmental studies.

5.6 Limitations and Future Directions

In addition to some limitations of the specific empirical work that were discussed in the relevant sections of each empirical chapter, overall findings of the current thesis should also be considered in light of some of the overall limitations discussed below. This section will also provide some future directions which could improve our understanding of SoA.

Firstly, this thesis used measures that have been suggested to reflect agency experience implicitly (for reviews: Haggard., 2017; Hughes et al., 2013; Moore & Obhi, 2012). However, two levels of agency experience have been suggested and these implicit measures might not reflect the higher-level judgements of agency. These are, feeling of agency which is the background feeling of being in charge of our actions, and judgement of agency which is the high-level experience of agency that emerge when we make conscious decisions about our agency (Synofzik et al., 2008). The measures used in thesis such as intentional binding and sensory attenuation reflects this low-level feeling of agency (Moore, 2016; Haggard, 2017). Therefore, developmental trajectories found in this thesis might not reflect the developmental trajectory of explicit judgements of agency. Nevertheless, our finding that shows increased implicit agency in children compared to late-adolescent (18-20 years old) is consistent with explicit agency studies suggesting increased self-agency judgements in children compared to adults (discussed in section 3.5, Metcalfe et al., 2010; Van Elk et al., 2015). Age of the adult groups in these studies are similar to our late-adolescent age groups (mean = 20 in Van Elk et al., (2015) and participants are 18-24 years old in Metcalfe et al., (2010)). Although the studies presented in this thesis (Chapter 3) represents some similarities with the explicit agency studies, future studies investigating implicit and explicit agency together with a developmental approach focusing on the adolescence can be useful to understand how (e.g. similar or diverging developmental trajectories) these two levels of agency develop in the transition from adolescence to adulthood.

Second, we only used a simple stimulus, a beep sound, as the auditory stimulus in our tasks (Chapter 2, 3 and 4) and simple visual stimulus, a white flash (used in Chapter 2). These basic stimuli were used as action outcomes to study agentic experiences. However, in everyday life our actions usually lead to negative or positive valued, such as rewarding or punishing, outcomes. Therefore, the developmental trajectory and neural basis of agency can be differential when rewarding, punishing, emotional or socially relevant stimuli are used. This might be particularly important for adolescent population where there is an increased responsivity to both rewarding and aversive stimulus and increasing importance of peer groups (Casey, 2015). Also, use of the stimuli which have a value can influence how temporal recalibration processes integrate the emotional aspects of outcomes to actions in different modalities (e.g. emotional stimulus might have differential reflections in auditory and visual sensorimotor temporal recalibration). Nevertheless, the empirical studies presented in this thesis provide the basis for understanding SoA for neutral and basic stimulus on which future studies examining the effects of emotional stimulus and reward processing can be built.

Third, in the current thesis we increased the delay duration between action and the outcome from 250 ms in Chapter 3 to 450 ms in Chapter 4. This was done based on previous studies suggesting that increasing the delay duration around 400-500 ms would eliminate the possible motor contamination on the ERPs that are involved in outcome processing, the auditory N1 and P2 (Hughes et al., 2013a; Hughes & Waszak, 2011; Poonian et al., 2015). Although this approach possibly prevented the significant influences of motor contamination on N1 and P2 ERPs, this increase of delay duration might be the reason why we observed different developmental trajectories across the two empirical studies, especially in adults. Therefore, temporal contiguity difference between action and outcomes should be considered when interpreting the results from Chapter 3 and Chapter 4. This issue can be resolved in future EEG studies by using 250 ms delay duration and including an action only condition where participants make a button press action which does not lead to an outcome. This technique has been successfully used in some sensory attenuation studies by subtracting the motor related activity in the action only condition from the activity in the action outcome condition (e.g. Baess et al., 2008). It might be also useful to compare the developmental trajectories of short and long delay durations to understand the developmental effects on SoA for temporally close or distant consequences of our actions.

The studies presented in this thesis, to my knowledge, are the first studies investigating SoA from childhood through adolescence to adulthood. Hence, it is important that these findings are replicated in the future studies. This is especially because our findings in Chapter 3 and Chapter 4 showed some inconsistencies in terms of the developmental trajectory observed from late-adolescent to adult group, although the results were similar up-to late adolescence. That is, developmental trajectory of intentional binding was increasing in Chapter 3 and decreasing in Chapter 4 from late-adolescence to adulthood. This difference might be explained by the different temporal contiguities (250 ms versus 450 ms) across two studies in this thesis. However, replicating these findings and possibly extending them by adding these delay durations as a variable in the design could help to understand the developmental trajectory of implicit agency at different temporal contiguities. Furthermore, although this thesis used a wide range of the developmentally different age groups with sharp age ranges to benefit the quick nature of the cross-sectional studies (children: 9-10, mid-adolescents: 13-14, late-adolescents: 18-20 and adults: 25-28 years-old) replicating these findings in a longitudinal design could extend these findings by showing how a group of people's agentic experiences change over time. However, it should be considered that the transition from adolescence to adulthood is a long period of time (from puberty to mid-twenties) which can increase the study costs, time and drop rates from the study. Therefore, accelerated longitudinal study approach (investigating intentional binding in different age groups for a number of years) might be more cost effective to provide a replication and show how implicit agency change over time for different age groups.

The empirical work presented in this thesis highlighted adolescence as a critical developmental period for SoA. As discussed in the cue integration approach in Chapter 1 (section 1.4.3), a weighted combination of retrospective and predictive components depending on their reliability might be a key factor for a reliable agency experience. We argued that, U-shaped trajectory of intentional binding from childhood to adulthood might reflect a developmental shift from relying on retrospective to predictive components from childhood to adulthood (discussed further in section 3.5). This hypothesis should be tested in the future studies possibly by examining both retrospective and predictive processes in the transition from adolescence to adulthood (e.g. manipulating the reliability of outcome occurrence as in Moore & Haggard 2008). For instance, the probability of the outcome occurrence can be manipulated (e.g. actions lead to outcomes with 50% or 70%) and included as within subject variable together with the age groups included in this thesis. As seen in Moore and Haggard, (2008) in high probability condition, participants would show intentional binding effect even in the trials actions do not lead to outcomes. This would suggests that predicting an outcome would be enough to observe binding effect. In the low predictability condition, participants would show intentional binding effect only in the conditions where actions lead to outcomes suggesting participants waited for actually observing the outcome (retrospective) since outcome was not reliably predictable. This would help to investigate the predictive and retrospective constituents of intentional binding and it can show how these constituents develop throughout adolescence. Alternatively, predictive processes can be investigated using ERP components related to these processes (e.g. readiness potential, N1 and P2 attenuation) as in Chapter 4. However, it might be better to manipulate temporal contiguity (250ms and 450ms) between actions and the outcomes since predictive processes might be working in shorter intervals (also see Chapter 4). This could have implications for understanding impaired predictive processes and retrospective over-binding observed in schizophrenia a neurodevelopmental disorder, since this transitional period is where we observe increased vulnerability for its emergence (Gomes et al., 2017; Harrop & Trower, 2001).

Although the current thesis contributes to our understanding of agency, its neural basis and correlates especially during the transition from adolescence to adulthood using tDCS and EEG, other techniques can be useful to understand this developmental effect and its underlying neural circuits. Future neuroimaging studies such as functional magnetic resonance imaging (fMRI) studies could be useful for revealing where and how these developmental differences occur in the brain throughout adolescence. For instance, fronto-parietal network has been suggested to underline the agency experience (discussed in section 1.5); however, the recruitment of these areas can be different and/or additional areas can be recruited based on the developmental stage and their maturation. Hence, such future studies, which can be built on the current thesis, would be useful for understanding the neural basis and development of SoA.

5.4 General Conclusions

The current thesis aimed to investigate the development and brain mechanisms of SoA during the transition from childhood to adulthood with a focus on adolescence. To do this, it used a variety of phenomena that are central to SoA (temporal recalibration, intentional binding and sensory attenuation) and a variety of techniques and perspectives (tDCS, EEG, behavioural and developmental approach). This thesis added to the current knowledge by providing a number of novel findings. First, it provided first direct evidence that sensorimotor temporal recalibration can be modulated by a non-invasive brain stimulation technique and sensory specific brain areas might be at play during sensorimotor temporal recalibration (Chapter 2). Second, it showed that SoA as indexed by intentional binding might have a U-shaped developmental trajectory, (as measured by the Libet Clock method) from childhood to adulthood and it reaches the lowest level during late-adolescence (Chapter 3). This suggests an increased agency experience in childhood and adulthood with a decrease during mid and late-adolescence. The developmental trajectory observed was due to developmental changes in outcome binding, not action binding. This suggests a much more prolonged development for outcome binding processes. Furthermore, the results from the studies reported also showed that intentional binding can be susceptible to the features of the method that is being used to measure it and Libet Clock method might be more advantageous to use since the results reported in this thesis showed that it might be more stable and easier to perform compared to Stream of Letters method (Chapter 3). Further investigating the development and neural correlates of implicit agency using EEG showed that mid-adolescents have greater levels of implicit agency experience compared to adults and it becomes adult-like during late-adolescence (Chapter 4). The ERP data suggested that this increased implicit agency observed in mid-adolescence may be mediated by a specific neural process acting to over-attenuate their action outcomes (as measured by P2 attenuation) with an over-reliance on the neural activity that is leading to their voluntary actions (late readiness potential). The findings across two chapters investigating developmental trajectory of implicit agency suggested that temporal contiguity (short and long delay durations used in Chapter 3 and 4 respectively) might cause differential developmental trajectories that should be further investigated and replicated in future studies. Nevertheless, they, overall, suggested that adolescence might be a critical period for the development of implicit SoA. Overall, developmental approach with a focus on adolescence used in this thesis provided a novel approach for understanding the development of SoA and its underlying mechanisms as well as understanding adolescent behaviour (e.g. increased risk-taking behaviour during adolescence).

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Appendix – Supplementary Tables

Supplementary Table 1. *N1 and P2 amplitudes for each condition and age-group, and N1 and P2 attenuation for each age-groups. Standard error of the mean presented in brackets*

	N1 and P2 amplitudes in Beep-Only condition						**N1 and P2 amplitudes in Action-Beep condition**						**N1 and P2 Attenuation**					
	Mid-Adolescent		**Late-Adolescent**		**Adult**		**Mid-Adolescent**		**Late-Adolescent**		**Adult**		**Mid-Adolescent**		**Late-Adolescent**		**Adult**	
	N1	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**	**N1**	**P2**
FC3	-5.62 (.75)	4.56 (.65)	-5.11 (.77)	1.70 (.68)	-4.77 (.77)	3.09 (.68)	-3.96 (.51)	1.79 (.40)	-3.50 (.53)	1.07 (.42)	-3.71 (.53)	2.30 (.42)	-1.65 (.49)	2.76 (.48)	-1.60 (.51)	0.62 (.50)	-1.05 (.51)	.787 (.50)
C3	-6.08 (.73)	5.95 (.66)	-5.17 (.75)	2.36 (.68)	-5.08 (.75)	2.93 (.68)	-4.42 (.50)	2.11 (.39)	-3.04 (.52)	1.74 (.40)	-3.19 (.52)	2.86 (.40)	-1.66 (.43)	3.84 (.59)	-2.13 (.45)	0.62 (.61)	-1.89 (.45)	0.06 (.61)
CP3	-4.49 (.51)	3.81 (.52)	-3.17 (.51)	1.03 (.54)	-3.56 (.51)	1.13 (.54)	-2.98 (.34)	2.13 (.32)	-1.77 (.36)	1.38 (.33)	-2.13 (.36)	1.75 (.33)	-1.50 (.30)	1.67 (.49)	-1.39 (.31)	-0.35 (.51)	-1.43 (.31)	-0.61 (.51)
FCz	-8.50 (1.12)	12.50 (1.27)	-9.92 (1.16)	9.21 (1.32)	-8.43 (1.16)	9.30 (1.32)	-4.23 (.62)	7.02 (.66)	-4.84 (.64)	4.34 (.68)	-3.99 (.64)	5.39 (.68)	-4.27 (.88)	5.47 (1.00)	-5.08 (.91)	4.87 (1.04)	-4.43 (.91)	3.90 (1.04)
Cz	-7.62 (1.13)	18.94 (1.46)	-9.85 (1.17)	11.74 (1.74)	-7.84 (1.17)	10.26 (1.52)	-4.21 (.59)	8.97 (.72)	-4.79 (.61)	5.98 (.75)	-4.25 (.61)	6.56 (.74)	-3.41 (.82)	9.97 (1.11)	-5.06 (.85)	5.76 (1.15)	-3.59 (.84)	3.70 (1.15)
CPz	-4.02 (.73)	14.23 (1.14)	-5.40 (.76)	8.51 (1.18)	-4.91 (.75)	7.32 (1.18)	-2.85 (.43)	7.56 (.61)	-2.78 (.45)	5.00 (.64)	-3.00 (.44)	5.03 (.64)	-1.17 (.54)	6.67 (.86)	-2.62 (.56)	3.50 (.89)	-1.91 (.56)	2.28 (.89)
FC4	-5.97 (.68)	4.42 (.65)	-6.35 (.70)	3.46 (.67)	-4.07 (.70)	3.65 (.67)	-3.04 (.45)	3.64 (.50)	-4.12 (.47)	1.77 (.52)	-3.00 (.47)	2.99 (.52)	-2.93 (.54)	0.78 (.53)	-2.22 (.56)	1.68 (.55)	-1.07 (.56)	0.65 (.55)
C4	-6.18 (.57)	4.73 (.66)	-6.36 (.59)	3.93 (.68)	-4.08 (.59)	3.76 (.68)	-3.60 (.34)	3.35 (.43)	-3.71 (.35)	2.36 (.45)	-3.00 (.35)	2.85 (.45)	-2.58 (.50)	1.38 (.55)	-2.64 (.52)	1.56 (.57)	-1.07 (.52)	0.90 (.57)
CP4	-4.70 (.47)	3.58 (.62)	-3.95 (.48)	2.75 (.65)	-2.75 (.48)	2.95 (.65)	-2.35 (.28)	3.48 (.42)	-2.03 (.29)	2.13 (.44)	-1.82 (.29)	2.66 (.44)	-2.34 (.46)	0.10 (.51)	-1.92 (.48)	0.62 (.53)	-0.92 (.47)	0.29 (.53)