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DIREKTOR: Univ.-Prof. Dr. T. Kircher

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Behavioral and Neural Indices of Perceiving Multisensory Action Outcomes

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M.Sc. Belkis Ezgi Arikan Seefeldt aus Izmir

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TABLE OF CONTENTS

SUMMARY

Distinct perception for voluntary vs. externally-generated action outcomes has been demonstrated in timing and intensity domains. First, time interval between an action and its outcome is perceived shorter. Second, sensory stimuli triggered by one's own action is judged as less intense than similar stimuli triggered externally. The differential perception of voluntary action outcomes has been attributed to efference copy-related predictive mechanisms, and has been studied extensively using behavioral and imaging methods. However, although voluntary movements in the real world produce feedback in multiple modalities, previous experiments mostly investigated unimodal action outcomes. Therefore, the perception of multisensory inputs associated with our own actions remains to be explored. The aim of this dissertation was to fill this gap by investigating the behavioral and neural correlates of multisensory action outcomes. In Study 1, synchrony perception for multisensory outcomes triggered by voluntary vs. externally-generated movements was assessed. Study 1.1 showed increased perception of simultaneity for audiovisual stimulus pairs around the time of action. Study 1.2 revealed a similar effect also when the movement was externally-generated, underlining the importance of causal relations between events in shaping time perception. Interestingly, the slopes of the psychometric functions in the voluntary condition were significantly steeper than the slopes in the externally-generated condition, suggesting a role of action-related predictive mechanisms in making synchrony perception more precise. Study 2 investigated the neural correlates of perceiving unimodal vs. bimodal inputs triggered by voluntary button presses compared with passive viewing of identical stimuli. Results showed BOLD suppression for voluntary action outcomes in comparison to passive viewing of the same stimuli. This BOLD suppression effect was independent of the to-be-attended modality and the number of modalities presented. The cerebellum was found to be recruited more during bimodal trials and when a delay was detected. These findings support action-related predictive processing of voluntary action outcomes, demonstrating it also for multisensory action outcomes. The findings also indicate the cerebellum's role in error-related action outcome processing, and the influence of the additional sensory modality on error-related activity in the cerebellum. Study 3 investigated neural correlates of perceiving unimodal vs. bimodal action outcomes by focusing on efference copy-related predictive processing in a naturalistic experimental set-up. Results extend findings of Study 2 regarding the predictive processing of multisensory action outcomes to a naturalistic context, and support the role of the cerebellum in error-related action outcome processing. Importantly, activity in the cerebellum was modulated by the additional modality, highlighting the role of multisensory processing in shaping motor-sensory interactions. Together, findings of these studies strengthen existing evidence on the distinctive perception for voluntary action outcomes, extending it to multisensory action outcomes, and to a realistic context. Implications of this line of research extend to revealing mechanisms behind agency deficits frequently observed in schizophrenia, as well as to the development of intervention techniques targeting the rehabilitation of patients with spinal cord injury or stroke.

ZUSAMMENFASSUNG

Studien haben gezeigt, dass es Unterschiede in der Wahrnehmung von Handlungskonsequenzen gibt, abhängig davon ob die Handlung eine eigene, willkürliche Bewegung ist oder extern generiert wurde. Zum Beispiel wird die Zeit zwischen eigenen Handlungen und deren Konsequenzen kürzer wahrgenommen, als sie eigentlich ist. Des Weiteren werden sensorische Stimuli, die aus eigenen Handlungen entstehen, als weniger intensiv wahrgenommen als extern erzeugte Stimuli. Als Grund für die unterschiedliche Wahrnehmung von eigenen und extern generierten Handlungskonsequenzen vermutet man den Efferenzkopiemechanismus. Dieser wurde bereits vielfach mittels behavioralen und bildgebenden Methoden untersucht. Wenn auch willkürliche Bewegungen in der ‘realen Umwelt’ Rückmeldungen an das Gehirn über verschiedene Modalitäten nach sich ziehen, haben bisherige Untersuchungen lediglich unimodale Handlungskonsequenzen untersucht. Daher ist die Wahrnehmung von multisensorischen Inputs der eigenen Handlungskonsequenzen, ein noch unerforschtes Thema. Das Ziel dieser Dissertation ist es, diese Lücke zwischen behavioralen und neuronalen Korrelaten multisensorischer Handlungskonsequenzen zu schließen. In der ersten Studie wurde die synchrone Wahrnehmung von multisensorischen Konsequenzen untersucht, welche durch willkürliche oder extern erzeugte Handlungen ausgelöst wurden. Studie 1.1 zeigte eine gesteigerte Wahrnehmung von Simultanität der audiovisuellen Stimulipaare über die Zeit der Handlung auf. Studie 1.2 konnte einen ähnlichen Effekt bei extern generierten Bewegungen zeigen. Dies unterstreicht die Rolle der zeitlichen Abfolge der Ereignisse für die Zuweisung von Kausalität. Der unterschiedliche Effekt der willkürlichen Handlungen manifestiert sich in der Genauigkeit der Bewertung ihrer Simultanität. Interessanterweise waren die Steigungen der psychometrischen Funktionen bei den Bedingungen mit willkürlicher Bewegung signifikant steiler als in der Bedingung mit extern-generierter Bewegung. Dies lässt eine Rolle von Efferenzkopiemechanismen bei der Wahrnehmung von Simultanität vermuten. Die zweite Studie untersuchte die neuronalen Korrelate der Wahrnehmung von unimodalen und bimodalen Handlungskonsequenzen bei willkürlichem Tastendrücken im Vergleich zur passiven Beobachtung der identischen Handlungskonsequenzen, ohne diese verursacht zu haben. Die Ergebnisse zeigen eine BOLD-Unterdrückung bei willkürlichen Handlungen verglichen mit der Bedingung des passiven Beobachtens der Stimuli, unabhängig von Modalität der Stimuli, auf welche die Aufmerksamkeit gerichtet war. Das Cerebellum scheint eine zentrale Rolle in bimodalen Bedingungen zu spielen, v.a. in der Detektion von Verzögerungen zwischen den Stimuli der Modalitäten. Diese Ergebnisse zeigen eine distinkte neuronale Wahrnehmung willkürlicher Handlungen, bei der Verarbeitung von Multisensorischen Reizen. Die dritte Studie untersuchte die neuronalen Korrelate der Wahrnehmung von uni- vs. bimodalen Handlungskonsequenzen mit Fokus auf Efferenzkopiemechanismen in einer naturalistischen experimentellen Umgebung. Die Ergebnisse stützen die zuvor aufgeführten Befunde im Bezug auf Efferenzkopiemechanismen bei der Wahrnehmung von selbstgenerierten Handlungskonsequenzen, und erweitern diese Befunde für einen multisensorischen Kontext. Weiterhin unterstreichen sie die Beteiligung des Cerebellums an Efferenzkopiemechanismen. Wesentlich ist hier, dass der modulatorische Effekt der zweiten Modalität auf das BOLD-Signal die Rolle von multisensorischen Prozessen bei motorsensorischen Interaktionen unterstreicht. Zusammen genommen bestärken die Studien die unterschiedliche Wahrnehmung von Handlungskonsequenzen willkürlicher Bewegungen und extern generierter Bewegungen und erweitern diese Befunde mit einem multimodalen Setting. Arbeiten aus diesem Gebiet können maßgeblich dazu beitragen, gestörte Zuweisungen von Urheberschaft bei Schizophrenie besser zu verstehen. Des Weiteren kann ein besseres Verständnis dieser Prozesse dazu beitragen, Patienten mit Rückenmarksverletzungen oder Schlaganfall effizienter behandeln zu können.

ABBREVIATIONS

ACC: anterior cingulate cortex

AV: audiovisual

BOLD: blood-oxygen-level dependent

fMRI: functional magnetic resonance imaging

IPL: inferior parietal lobule

MTG: middle temporal gyrus

PMD: passive movement device

SMA: supplementary motor area

SJ: simultaneity judgment

SOA: stimulus onset asynchrony

STG: superior temporal gyrus

1 INTRODUCTION

This dissertation aims to fill the gap in our existing knowledge on action perception by bringing multisensory nature of action outcomes to focus. This is important, since most goal-directed actions lead to multiple sensory inputs, which need to be integrated not only to each other but also to the action that triggers them. The Introduction is organized to provide an overview of the literature on action outcome processing and multisensory perception in an attempt to reconcile these two research areas. In this respect, it mainly explains why voluntary action outcome processing is considered unique, how it manifests itself on a behavioral and neural level, and how multisensory processing is relevant to understand voluntary action outcome processing. At the end, questions remained to be investigated are mentioned, some of which were addressed in this dissertation.

1.1 The interplay between perception and action

1.1.2 Perception and action as reciprocal experience

"Perception is not something that happens to us, or in us. It is something we do."

Alva Noë, Action in Perception (Noë , 2004, p.1)

The above quote from Alva Noë highlights the notion that perception is not a one-way process in which events taking place in the environment are passively encoded. Perception is, on the contrary, a product of our interactions with the world surrounding us, realized through active inquiry and exploration. In this sense, a reciprocal relationship between our actions and perception exists in making sense of ourselves and the external world (Wagman, 2008).

There are fundamentally two ways in which humans interact with their environment. This can be either through manipulating the world to produce desired states, or by accommodating one’s goals to environmental demands (Herwig et al., 2007; Prinz, 1997). While the former is termed as voluntary, intention-based or operant in which the agent aims to produce a desired goal, the latter is termed as reaction, stimulus or response-based which allows for adapting to changes in the environment (Herwig et al., 2007; Prinz, 1997). To put it simply, the difference lies in whether an action is voluntary or externally-generated. Voluntary actions are characterized by their goal-directedness in that they aim towards producing internally pre-specified effects (Herwig et al., 2007). Although the attribute of 'intentionality' regarding voluntary movements not as straightforward as it seems (Haggard and Eimer, 1999; Libet et al., 1983b), it is useful to differentiate actions triggered by more readily observed external inputs from those that seem to be more under one's control. Moreover, voluntary and externally-generated actions are rarely dichotomous in everyday experience, with both movements representing two different ends of a continuum (Krieghoff et al., 2011). Nevertheless, a classification based on the dichotomy would allow one to investigate the fundamental differences between these actions.

Since most of our everyday actions involve a voluntary component, substantial amount of research has explored in detail the interplay between voluntary movements and their sensory outcomes. In general, existing evidence indicates a unique manner in which voluntary actions and their outcomes are processed.

1.1.3 Perceiving sensory outcomes of voluntary actions: what is unique about it?

Research on voluntary actions and their sensory outcomes has consistently shown that self-generated inputs are perceived differently than those inputs triggered externally (Blakemore et al., 1999, 1998; Haggard et al., 2002). These perceptual effects are mainly observed in two domains: perceived timing for action outcomes and perceived intensity of the sensory effect.

First domain concerns the subjective experience of time regarding the voluntary action and its effect. Perceived timing between a voluntary action and its sensory outcome has been found to be distorted. A seminal study by Haggard, Clark, & Kalogeras, (2002) demonstrated that perceived timing of voluntary actions and their sensory outcomes are attracted towards each other. This effect is termed as intentional binding, and has been established in other experiments (Engbert et al., 2007; Haggard and Cole, 2007). It has also been demonstrated that temporal discrimination regarding the voluntary movement and its outcome is impaired immediately after the action, not later during the action outcome phase (Wenke and Haggard, 2009). In addition, temporal predictability, namely the predictability of the interval between the action and the outcome, and contiguity of the action outcome contribute to the intentional binding effect (Cravo et al., 2011; Haggard et al., 2002). Nevertheless, intentional binding seems to be specific to voluntary actions, as individual factors found to influence binding are not sufficient for the effect to occur (Cravo et al., 2011; Engbert et al., 2007; Haggard et al., 2002; Wohlschläger et al., 2003).

Second domain regarding the differential processing of voluntary action outcomes concerns perceived intensity of sensory inputs triggered by voluntary actions. Accordingly, sensory outcomes generated by one’s own movements are perceived as less intense compared with equivalent sensory inputs that are externally-generated (Blakemore et al., 1998; Sperry, 1950; Von Holst, 1950; Weiskrantz et al., 1971; Wolpert et al., 1995). This phenomena is known to as sensory suppression (or sensory attenuation), and has been found to manifest itself both on a behavioral (Bays et al., 2005; Blakemore et al., 1998; Cardoso-Leite et al., 2010) and neural level (Baess et al., 2008; Blakemore et al., 1998; Hughes et al., 2013; Hughes and Waszak, 2011; Shergill et al., 2013). In addition, support for the existence of sensory suppression comes from several studies using different methodologies. In their comprehensive review on sensory suppression, Hughes, Desantis, & Waszak (2012) list studies using subjective report (Blakemore et al., 1999), signal detection methodology (Cardoso-Leite et al., 2010), and subjective equality judgments (Sato, 2008), among others (Bays et al., 2005; Voss et al., 2007). Moreover, sensory suppression has been shown to occur for somatosensory (Bays et al., 2005; Blakemore et al., 1998; Voss et al., 2008), auditory (Aliu et al., 2009; Baess et al., 2011, 2008; Horváth et al., 2012; Knolle et al., 2012; Schafer and Marcus, 1973; Timm et al., 2014) and visual (Cardoso-Leite et al., 2010) modalities.

In order to illustrate mechanisms underlying intentional binding and sensory suppression, two influential theoretical perspectives have been proposed, namely the ideomotor theory and forward models.

1.2 Mechanisms underlying action outcome perception

1.2.1 Ideomotor theory

Although the history of ideomotor theory goes back to the mid-1800s, it has begun to be considered as a legitimate scientific framework during the 1970s, as behaviorism restricted its study (for reviews, see Shin, Proctor, & Capaldi, 2010; Stock & Stock, 2004). Greenwald (1970) and Prinz (1987) were the modern pioneers of the ideomotor framework and its experimental investigation. Ideomotor theory of action control attempts to explain the origin of voluntary actions with regard to their perceivable effects. It posits that goal-directed actions are selected, initiated and executed with respect to their sensory outcomes (Prinz, 1997; Walter and Rieger, 2012). To put it differently, voluntary actions are characterized by their anticipated effects, which stems from a bidirectional association between sensory representations and motor commands of the action (Elsner and Hommel, 2001; Greenwald, 1970; Herwig et al., 2007; Prinz, 1997; Waszak et al., 2012). In this sense, the idea of an action’s sensory effect is equivalent to the actual movement, hence the term ‘ideomotor’ (James, 1950). It is therefore claimed that action selection depends on the sensory outcome that is predicted to trigger, via learned action-effect associations (Waszak et al., 2012). Several studies have provided corroborative evidence for the ideomotor principle (Elsner et al., 2002; Elsner and Hommel, 2004, 2001; Herwig et al., 2007; Kunde, 2001). These studies mainly demonstrated that when a certain association is formed between an action and a sensory event, anticipating the action effect impacts behavior.

Although contemporary ideomotor approaches maintain the assumption of a direct association between an action and its anticipated effect acquired through learning, the nature of these associations necessitates more evidence. Furthermore, despite substantial evidence supporting the ideomotor view, these theories have been claimed to downplay one important aspect: the movement itself (Chambon and Haggard, 2013). This aspect is incorporated in forward models of motor control which attempt to clarify mechanisms behind voluntary actions and their sensory outcomes.

1.2.2 Forward models of motor control

Recent computational motor control theories attempt to elucidate the relation between voluntary movements and their sensory outcomes in terms of internal and forward models. Accordingly, goal-directed actions result in peripheral and central signals. Distinguishing these signals is of high relevance to the organism because it allows for recognizing the outcomes of self-generated actions as separate from those outcomes generated externally, providing more efficient processing of external inputs that might likely harm the individual as opposed to inputs arising as a result of one's own action (Blakemore et al., 1998; Desmurget and Grafton, 2000; Wolpert et al., 2001; Wolpert et al., 1995). Moreover, such a system enables a highly accurate representation of movements and their sensory outcomes, promoting the learning of action outcome associations and ensuring that the desired goal state is attained (Frith et al., 2000).

Goals can be achieved by a central monitoring mechanism which consists of internal models that represent aspects of one's own body and the external world (Frith et al., 2000; Wolpert, 1997; Wolpert et al., 1995). Forward (predictors) and inverse (controllers) models correspond to different models the organism utilizes to achieve the desired state. Whereas an internal forward model is used to acquire the causal relation between events by predicting the next state of the system, inverse models are used to determine motor commands required to attain a certain sensory outcome. Forward models accomplish this by using an efference copy of the motor command in order to anticipate and modulate the processing of sensory outcomes resulting from the action. The motor command needed for the desired state change is produced by the inverse model (Miall and Wolpert, 1996; Sperry, 1950; Von Holst, 1950; Wolpert et al., 1998). Such a mechanism can be used to 1) compensate for delays that likely occur within sensorimotor loops due to differences in neural transduction or processing delays, 2) anticipate and cancel expected sensory outcomes of a movement caused by oneself (sensory re-afference), 3) transform sensory errors between expected and actual sensory feedback into motor command errors, promoting sensorimotor learning, and 4) optimally estimating the current state of the system (Davidson and Wolpert, 2005; Doya, 1999; Frith et al., 2000; Wolpert et al., 1998, 1995; Wolpert and Flanagan, 2001). As stated above, forward models explain sensory suppression as the result of a match between the actual and the desired state of the system (Blakemore et al., 1998; Wolpert et al., 1998). In case of a discrepancy, the system needs to either update predictions regarding the action outcome relation, or attribute the source to an external event (Blakemore et al., 1999).

An important role attributed to the forward model concerns the sense of agency, namely the subjective experience of being in control of one's own actions and the outside world one aims to manipulate (Chambon and Haggard, 2013; Moore, 2016). In addition to allowing external unexpected events to have prioritized processing, sensory suppression has been linked with the formation of sense of agency (Chambon and Haggard, 2013; Frith et al., 2000; Hughes et al., 2012). For example, Tsakiris et al. (2005) demonstrated that efferent information contributes to self-recognition, and neither visual nor proprioceptive feedback arising from one's action is sufficient for generating the effect. Indeed, it has been demonstrated that the efferent motor command is a necessary component for agency to occur (Engbert et al., 2007; Haggard and Cole, 2007). Intentional binding has been proposed as an implicit measure of agency over sensory events, suggesting that binding results from motor prediction mechanisms (Haggard et al., 2002; Tsakiris and Haggard, 2003).

1.2.3 Summary of ideomotor theories and forward models

Ideomotor theories and forward models share the common assumption that predictive relations between voluntary actions and their sensory outcomes underlie how these outcomes are processed and influence our perceptual experience as active agents. Both frameworks put high emphasis on the anticipatory nature of action outcome associations by positing that action effects can be predicted *before* they are experienced, through sensorimotor learning (Franklin and Wolpert, 2011; Shin et al., 2010; Wolpert and Flanagan, 2001). Intentional binding and sensory suppression are hypothesized to result from such a prediction mechanism (Hughes et al., 2012). However, the assumptions of these frameworks are still to be investigated. Neuroimaging offers a complementary means to reveal the link between voluntary actions and their sensory outcomes.

1.3 Neural correlates of perceiving voluntary actions and their outcomes

Voluntary actions comprise a series of processing stages which lead to the generation of conscious action experiences (Haggard et al., 2002). These stages include the intention and decision to move, generation and execution of motor commands, re-afferent feedback arising from the motor command and the use of this feedback for action monitoring (Haggard and Eimer, 1999; Libet et al., 1983b; Yarrow and Obhi, 2014). Neural correlates pertaining to these stages have been investigated using a variety of methodologies.

1.3.1 Planning and execution of voluntary actions

It has been demonstrated that the medial wall of the human cortex plays an important role in motor learning and control. More specifically, this region has been found to be involved substantially in planning, execution and selection of voluntary movements (Picard and Strick, 1996). Single cell recordings provided further evidence for the involvement of this area in motor preparation (Fried et al., 2011). Using functional magnetic resonance imaging (fMRI), several studies sought to better isolate areas specifically implicated in voluntary actions by contrasting these movements with externally-generated, involuntary, observed and/or imagined movements. Findings have revealed common as well as distinct mechanisms regarding the processing of these movements.

Voluntary and externally-generated movements both engage medial motor areas such as the supplementary motor area (SMA), pre-SMA and rostral cingulate zone (RCZ), contralateral primary motor and sensory cortices, insula, contralateral cerebellum, and parietal cortices (Ciccarelli et al., 2005; Cunnington et al., 2002; Szameitat et al., 2012; Weiller et al., 1996). Despite these commonalities studies also find relative or distinct involvement of these regions along with other brain structures in the generation of voluntary movements. Among them, frontostriatal circuit seems to be specifically involved in the planning, initiation and execution of voluntary movements. The frontostriatal circuit consists of dorsolateral prefrontal cortex (DLPFC), cingulate motor areas/anterior cingulate (ACC) and SMA (Cunnington et al., 2005, 2002; Deiber et al., 1999; Herwig et al., 2007; Jenkins et al., 2000a; Lau et al., 2004; Mueller et al., 2007; Weiller et al., 1996; Wiese et al., 2004). The premotor cortex on the other hand, seems to be involved in the general planning, programming, initiation, and guidance of simple and skilled motor tasks (Grèzes and Decety, 2001). More detailed evidence comes from event-related or time-resolved imaging studies, which provide invaluable information on particular areas recruited during each processing stage of the voluntary movement. Early movement-related potentials (MRPs), namely the cortical activity associated with a voluntary movement, have been found to precede the movement by several hundred milliseconds. Early components of MRPs are thought to reflect movement preparation whereas late components have been linked to movement execution (Cunnington et al., 1996). SMA is the area implicated in generating these potentials (early MRP), suggesting its role in motor preparation (Cunnington et al., 1996). Other studies provide further evidence for the specific involvement of the rostral region of the SMA (pre-SMA) in early phases of movement preparation (Cunnington et al., 2002; Lee et al., 1999; Weilke et al., 2001; Wildgruber et al., 1997). In addition, pre-SMA seems to be implicated in action representation prior to movement execution (Cunnington et al., 2005; Picard and Strick, 1996). Aside from SMA, evidence exists for the role of cingulate motor areas in movement preparation. For example, part of the ACC (RCZ) has been found to be relevant for freely choosing an action, which is considered as one of the defining aspects of voluntary movements (Lau et al., 2004; Mueller et al., 2007).

Although above-mentioned investigations contributed extensively to our understanding of how we act purposefully, several limitations exist in disentangling the neural basis of voluntary movements. For example, baseline conditions that have been used as contrasts to voluntary movements are confounded by motor and perceptual differences. In an attempt to address these limitations, Mueller et al. (2007) adopted a paradigm from Waszak et al. (2005) which enabled them to compare internally and externally-generated actions while controlling for perceptual and motor confounds present in previous investigations. They found that whereas RCZ is specifically engaged during intentional movements, pre-SMA activity is present in both movements. Their results suggest the importance of dissociating ‘what’ and ‘when’ components inherent in the intention to move while controlling for common processes shared by different movements. (Krieghoff et al., 2009) provided supporting evidence for the findings of Mueller et al. (2007) by pointing to the interdependence between which action to perform and when to perform it. Together, these studies highlight the necessity to consider dissociable functions of the human cortex in performing voluntary actions, as well as interactions between these functions.

In addition to medial frontal areas, parietal areas have been implicated in the planning and execution of voluntary movements (Desmurget and Sirigu, 2009; Farrer et al., 2008; Fourneret et al., 2002; Haggard and Eimer, 1999; Lau et al., 2004; Lau et al., 2004; Libet et al., 1983b; Sirigu et al., 1999; Sirigu et al., 2004). This is supported by the finding that parietal cortex has functional connections with the premotor cortex (Andersen and Buneo, 2002; Assal et al., 2007; Desmurget and Sirigu, 2009; Farrer et al., 2008; Gold and Shadlen, 2007; Haggard, 2009; Sirigu et al., 1999; Sirigu et al., 2004). In a detailed study, Desmurget & Sirigu (2009) showed that the posterior parietal cortex stimulation is associated with the conscious intention to move even when the motor response is absent. This finding clearly underlies the importance of parietal cortex on the conscious intention to move.

In sum, action planning and execution engage several areas of the brain, some of which seem highly distinct for voluntary actions while other areas are recruited by a variety of movements. Despite mixed findings, several studies suggest distinctive processing for voluntary movements in pre-motor and parietal areas in action planning and execution.

1.3.2 Neural correlates of action outcome processing

In addition to distinct neural processing involved in the planning and execution of voluntary movements, sensory outcomes resulting from these actions are also processed differently in the brain. Recently, Kühn et al. (2011) showed that anticipating a certain movement activates not only motor-related areas, but also those areas responsible for coding of the movement’s expected sensory consequences. This and a number of other investigations stress the necessity of conceptualizing voluntary actions together with their learned sensory effects (Elsner et al., 2002; Melcher et al., 2008).

A number of studies focusing on the interplay between actions and their sensory outcomes examined the neural basis of sensory suppression and error-related processing of action outcomes. Earlier investigations by Blakemore et al. (1998; 1999) demonstrated that tactile sensations arising from self-generated movements vary as a function of the discrepancy between expected and predicted sensory effects. More specifically, they found that ratings of ticklishness of a tactile stimulus increase when temporal or spatial discrepancy exists between the actual and predicted outcome of the voluntary movement (Blakemore et al., 1998). This is reflected in the neural responses associated with perceiving the tactile feedback of the movement, by activation reductions in somatosensory areas when there is no discrepancy between the actual and the expected sensory feedback, suggesting suppression at a neural level (Blakemore et al., 2001; Blakemore et al., 1999).

An important question regarding the processing of action outcome associations concerns the contribution of efference copy signals. The region of interest which provides efferent signals to sensory cortices has been much of debate: some studies found support for the SMA as the area providing efferent signals (Haggard and Whitford, 2004), or the ventral premotor cortex (Christensen et al., 2007a), while others state cerebellum to be highly relevant for the generation of efferent signals (Blakemore et al., 2001; Blakemore et al., 1998; Knolle et al., 2013, 2012). Indeed, cerebellum has been proposed to act as a forward controller, transforming the predicted sensory goals into motor representations. Accordingly, the cerebellum generates efference copy signals under the current state of the system, producing not only an estimated motor output, but also of expected sensory outcomes generated by these outputs (Wolpert et al., 1998). In line with this assumption, this area has been shown to play a role in modulating sensory outcomes of motor commands, providing an error signal used to cancel the somatosensory responses to voluntary movements (Blakemore et al., 2001; Blakemore and Sirigu, 2003; Miall et al., 1993). Apart from somatosensory action outcomes, Knolle et al. (2013, 2012) demonstrated that cerebellum generates predictions for auditory action outcomes. These findings support the assumption that sensory suppression results from predictive processing of action outcomes (Blakemore et al., 1998; Blakemore et al., 2000; Blakemore et al., 1998; Blakemore and Sirigu, 2003).

In addition to the SMA and the cerebellum, parietal cortex has been implicated in action outcome processing. Convincing evidence exists on the distinct involvement of this area in processing self-generated inputs (Christensen et al., 2014; MacDonald and Paus, 2003; Sirigu et al., 1999). This is supported by the finding that activity in the parietal cortex is linked to the processing of temporal and spatial errors between voluntary movements and their sensory outcomes (Leube et al., 2003a). There is also evidence for the relevance of this area in movement control (Rizzolatti et al., 1997). Furthermore, parietal cortex has been found to be involved in the integration of multisensory inputs (Graziano and Botvinick, 2002) as well as visuo-motor information (Christensen et al., 2007b). Angular gyrus, a region located in the parietal cortex, has been proposed as a candidate area for processing action outcome discrepancies (Farrer et al., 2008; Sirigu et al., 2004). This area has been implicated in the selection of intentional actions (Desmurget and Sirigu, 2009), with enhanced activity associated with decreased attribution of agency over events (Kühn et al., 2011). A recent study by Zwosta et al. (2015) also suggests a general involvement of this area in action outcome processing, not only in cases of discrepancy. Melcher et al. (2008) provided additional evidence for the involvement of angular gyrus in action outcome processing, along with the cerebellum. Therefore, studies suggest that areas of the parietal cortex and the cerebellum are highly implicated in representing the current and the predicted state of the system, resulting in sensorimotor integration and error-related action outcome processing (Frith et al., 2000).

1.4 State of the art and beyond: multisensory action outcomes and naturalistic action outcome relations

Recently there has been a growing interest in exploring how action and perception are interrelated in naturalistic settings (Ingram and Wolpert, 2011; Kingstone et al., 2008; Körding and Wolpert, 2004). This involves not only the utilization of virtual reality or tracking systems outside the laboratory to create more realistic action perception scenarios, but also the inclusion of aspects intrinsic to the action perception cycle in the real world.

First, more and more studies use computer-generated sensory feedback, virtual reality and tracking systems that allow measurement beyond the laboratory to examine the interplay between action and perception (Ingram and Wolpert, 2011; Kingstone et al., 2008). This is strikingly different than previous studies in which an action is highly restricted in its execution as well as its effects. Even though we live in a highly computerized environment, we still need to be able to acknowledge actions we perform in our everyday lives which are highly characterized by complex movement sequences. In addition, sensory feedback generated by our actions are also not as simplistic as in most experimental settings.

Therefore, incorporation of these features to research paradigms is a crucial step in understanding everyday actions and accompanying perceptual experience.

Another issue regarding ecological validity concerns the nature of our daily actions. Although research on action outcome processing usually involves an action triggering sensory input from a certain modality, our actions often lead to multiple sensory outcomes. Combining sensory information from different modalities is crucial in order to have a meaningful representation of the world (Driver and Spence, 2000). As regards multisensory processing, current approaches also manifest a growing interest in exploring naturalistic situations (Chandrasekaran et al., 2009; Senkowski et al., 2007). Various animal and human studies have established that sensory processing is not modular, and sensory modalities interact with each other in early phases of sensory information processing (for a review see Shimojo and Shams, 2001). Neural underpinnings of multisensory processing provide additional insights into how information arriving from different senses interact. Previously, it has been assumed that a hierarchical processing scheme exists in which sensory-specific brain areas are devoted to the processing of sensory stimulus of a particular modality at an early stage, while higher order multisensory convergence zones (areas of the brain receiving afferent inputs from different senses) are involved in processing multisensory information in later stages (Macaluso, 2006). More recent investigations suggest that the so-called sensory-specific areas are also responsive to stimuli from other modalities, and multisensory processing indeed begins at early stages of information processing (Driver and Noesselt, 2008; Macaluso, 2006; Shimojo and Shams, 2001). These investigations have also provided convincing evidence for enhanced behavioral performance (i.e., heightened perceptual awareness, decreased reaction times) coupled by increases in cortical activity related to sensory processing (Foxe et al., 2000; Giard and Peronnet, 1999; McDonald et al., 2000; Stein et al., 1996; Vroomen and de Gelder, 2000). Converging sensory inputs providing information about a single event seems to underlie this enhancement (Driver and Spence, 2000). In addition, there is evidence that such enhancement can also be observed even when a stimulus provides no information about the other sensory modality (Giard and Peronnet, 1999; McDonald et al., 2000; Stein et al., 1996; Vroomen and Gelder, 2004). On the other hand, just as a particular sensory modality can enhance the processing of another modality, it can also hinder its processing (Colavita, 1974; Kawashima et al., 1995; Meredith, 2002; Morein-Zamir et al., 2003; Sinnett et al., 2008; Wang et al., 2012). For example, Laurienti et al. (2002) found significant reductions in cortical activity linked to visual processing during the presentation of an auditory input and vice versa, possibly as a way of increasing the salience of a relevant sensory modality that seems more important in the processing hierarchy. In both cases, spatiotemporal correspondences as well as semantic congruencies between different sensory inputs seem to drive these effects (Murray et al., 2004; Senkowski et al., 2007).

The above-mentioned studies underlie the significance of investigating multisensory interactions, not only among different senses, but also in relation to our interactions with the external world. In the context of voluntary movements, very few studies addressed multisensory processing of action outcomes. Among these was an EEG study by Mifsud et al. (2016), which found that while auditory stimuli lead to suppressed ERPs as indicated by a decrease in the auditory N1 component, visual stimuli result in an opposite effect (increase in the early visual N145 component). This finding clearly suggests cross-modal differences regarding sensory modalities in relation to voluntary movements. Other studies focusing on multisensory interactions in the context of action outcome processing have provided evidence regarding distinct time perception between voluntary actions and their multisensory outcomes (Desantis and Haggard, 2016a, 2016b; Parsons et al., 2013; van Kemenade et al., 2016). Recently our group has investigated behavioral and neural indices of perceiving multisensory as opposed to unisensory movement outcomes, and found behavioral advantage (van Kemenade et al., 2016) as well as neural processing differences for multisensory action outcomes (van Kemenade et al., 2017). These findings provide further evidence for the importance of exploring multisensory action outcomes.

1.5 Summary of the literature and open questions

Ideomotor and forward model frameworks attempt to explain mechanisms behind action outcome perception by highlighting predictive processing of acquired action outcome associations, which is responsible for distinctive perceptual experience. In this sense, these theories emphasize predictive processing acquired by learned associations between actions and accompanying sensory inputs. Despite the fact that neuroimaging studies in recent years have contributed vastly to our understanding on the interplay between action and perception, several issues remain to be further investigated. These involve the role of multisensory influences on action outcome processing and naturalistic action outcome associations as a means to better understand real world situations.

2 AIMS AND HYPOTHESES

The aim of this dissertation was to address the multisensory aspect of voluntary action outcomes which is an integral part of our everyday experience, but which has so far been overlooked. In this respect, the aim of the present dissertation was to investigate behavioral and neural correlates of multisensory action outcome perception. Behaviorally, time perception for multisensory stimuli triggered by voluntary actions were assessed. Regarding neural correlates, brain regions associated with perceiving unimodal and bimodal sensory outcomes triggered by voluntary actions were assessed. Another aim was to explore these associations in a more naturalistic setting using more realistic action outcome relations.

Study 1 investigated synchrony perception for multisensory action outcomes as opposed to similar outcomes triggered externally. It was assumed that temporal asynchronies between multisensory outcomes are tolerated when these outcomes occur close to the action that trigger them, in other words, when actions and outcomes are temporally contiguous. In the case of externally-generated movements, absence of efference copy-related predictions would lead to decreased asynchrony tolerance, even when the stimuli are temporally contiguous with the action. Accordingly, the following hypotheses were tested in Study 1:

1. Perception of synchrony regarding multisensory stimuli is maintained despite temporal asynchronies, when the stimuli are triggered by a voluntary action.
2. Decrease in temporal contiguity between the voluntary action and the multisensory stimuli lead to decrease in synchrony judgments.
3. Perception of synchrony for multisensory stimuli is higher when the stimuli are triggered by a voluntary compared with an externally-generated movement.
4. Decreased temporal contiguity between the action and the multisensory stimuli results in decreased synchrony judgments for voluntary compared with externally-generated movements.

Study 2 and 3 focused on the neural correlates of perceiving unimodal vs. bimodal action outcomes. In Study 2, voluntary button presses leading to unimodal auditory or visual, and bimodal audiovisual (AV) inputs were presented. Systematic delays were induced between the button press and the sensory outcome in order to investigate how temporal discrepancies between actions and their outcomes would modulate accompanying neural responses. Participants were also asked to detect these delays, which would enable them to focus on the action outcome discrepancy, and allow for behavioral assessment of delay detection when the outcome was unimodal vs. bimodal. Voluntary trials were compared with a control condition in which same sensory inputs were presented after a cue, without the execution of an action. It was expected that sensory processing during voluntary actions would be suppressed. The detection of temporal discrepancies between the action and the outcome would also result in increased activity in areas associated with the updating of action outcome predictions (i.e. cerebellum), and more so with the additional modality which would presumably provide extra information on the temporal discrepancies. The specific hypotheses tested in Study 2 were as follows:

1. Neural responses to voluntary movement outcomes are suppressed compared with neural responses to passive viewing of identical sensory inputs.
2. Neural responses to voluntary movement outcomes are similar when the movement leads to unimodal vs. bimodal outcomes due to predictive processing of action outcomes.
3. Neural responses associated with subjective delay detection involve brain regions linked with processing error-related information regarding the predicted relation between the action and the outcome such as the cerebellum, as opposed to subjectively undelayed trials.
4. Neural responses associated with subjective delay detection are influenced by whether the action outcome is unimodal or bimodal.

Study 3 delved more into the question of action specific predictive processing of sensory outcomes by adopting externally-generated movements of the wrist as a comparison to voluntary hand movements. Accordingly, voluntary movements of the right hand leading to visual (via real time display from a camera) or AV feedback were compared with externally-generated movements of the hand. Such a set-up would also allow for a more naturalistic investigation of action outcome relations. Temporal delays were presented between the movement and the sensory outcome, and the participants were asked to detect delays between the actual movement and the visual feedback of the movement. As in Study

2, BOLD suppression would be expected when the movements were voluntary, with recruitment of areas specific to updating of predictions regarding voluntary action outcome associations, and increased error-related processing in bimodal trials compared with unimodal trials. The specific hypotheses that were tested in Study 3 were as follows:

1. BOLD suppression in sensory cortices occurs during voluntary movements compared with externally-generated movements.
2. Neural responses to unimodal and bimodal inputs associated with voluntary movements are similar independent of the modality received due to predictive processing of voluntary action outcomes.
3. Subjectively delay detection leads to increased error-related processing in areas such as the cerebellum as opposed to subjectively undelayed trials.
4. Neural activity correlated with subjective delay detection is impacted by movement and modality of the sensory outcome, i.e. increased error-related processing occurs for voluntary compared with externally-generated movements.

2.1 Overview of the Experimental Design

All studies in the present dissertation involved a voluntary movement leading to unimodal and/or bimodal sensory outcome/s. In all studies, different timing judgments were assessed. Because voluntary actions and their sensory outcomes are usually closer in time and/or can be predicted in time, manipulations in timing were hypothesized to lead to discrepancies between the action and the sensory outcome, influencing perceptual experience. In all experiments, a baseline condition was included to address action-related predictive processing of sensory outcomes. In Study 2, this was passive viewing of identical sensory stimuli triggered by the voluntary action, whereas in studies 1 and 3, it consisted of externally-generated movements in order to disentangle efference copy-related predictive processes specific to voluntary movements, from re-afferent sensory feedback present in both movements (for a review see Hughes et al., 2012). In Study 1, synchrony perception for multisensory action outcomes were examined by using simultaneity judgments, by coupling sensory inputs to voluntary and externally-generated movements. In Study 2, neural correlates of perceiving multisensory action outcomes were examined using voluntary button presses which triggered unimodal and bimodal visual and auditory outcomes as well as passive viewing of identical stimuli. Brain areas implicated in the processing of action outcome discrepancies were assessed by presenting systematic delays between the action and the outcome. In Study 3, neural correlates involved in perceiving multisensory action outcomes were explored by examining brain areas associated with the perception and error-related processing of voluntary vs. externally-generated movement outcomes using naturalistic action outcome relations.

3 STUDY 1: SYNCHRONY PERCEPTION FOR MULTISENSORY ACTION OUTCOMES

The content of Study 1 has been published as:

Arikan, B.E., van Kemenade, B.M., Harris, L.R., Straube, B., Kircher, T. (2017). Voluntary and involuntary movements widen the window of subjective simultaneity. Iperception 8(4), doi:10.1177/2041669517719297.

3.1 Background

Determining whether a clicking sound belongs to a light switch or a keyboard is one of the challenges the brain faces in response to the sensory events around it. Integrating sensory signals is necessary to form a coherent percept, and eventually a meaningful experience of the external world.

Although extensively studied on the perceptual level, research on multisensory interactions mainly focused on sensory stimuli that are external in nature (Alais et al., 2010). However, it has been well-documented that our actions shape how we perceive sensory stimuli compared with when they are spontaneously triggered. One phenomenon regarding this differential processing concerns the perceptual passage of time. In a seminal study by Haggard et al. (2002), it has been shown that there is a subjective compression of time between a voluntary movement and its consequence compared with when a movement is not intentional. More specifically, 'the perceived time of the action is shifted forwards towards the effect, and the time of the effect is also shifted backwards in time towards the action that caused it.' (Haggard and Cole, 2007, p. 212). This effect, known as intentional binding, has been replicated in later studies (Moore and Obhi, 2012; Tsakiris and Haggard, 2003). The tendency to bind voluntary actions to their effects was explained as a process that maintains a sense of agency (Haggard et al., 2002), or perceptual constancy (Yarrow et al., 2001). There is also evidence that intentional binding helps us build causal relations between actions and their consequences (Buehner and Humphreys, 2009a). Moreover, a recent study by Kawabe et al. (2013) emphasizes the importance of perceptual grouping between actions and their perception of causally related effects, suggesting that the resulting sense of agency can likely be explained by causality and cross-modal grouping.

Voluntary actions contain a certain sequence of processes to form a coherent stream of conscious action experiences (Haggard et al., 2002). These processes reflect the intention and decision to move, the generation and subsequent execution of the motor command, reafferent sensory feedback, and the use of this feedback for action monitoring (Haggard and Eimer, 1999; Libet et al., 1983a; Yarrow and Obhi, 2014). Interestingly, the perceived timing of actions appears to be different from the actual timing as measured by the cortical activity occurring well before movement onset (the readiness potential; Haggard et al., 1999; Libet et al., 1983a; Obhi et al., 2009; Yarrow and Obhi, 2014). If this information is present long before the movement, it could be used to generate predictions that are complete even before the movement occurs. Compatible with this idea, cells have been reported in the parietal cortex that adjust their response properties in anticipation of the post movement stimulation (Duhamel et al., 1992). The intentional binding effect is not present for involuntary movements or when the consequence of the action follows after an unpredictable delay (Haggard et al., 2002). These findings suggest that our motor system is used to make specific predictions of the effects they produce, influencing timing perception for these effects (Haggard, 2005). The perception of timing for actions and their effects have mostly been investigated using one sensory modality as the feedback of the action. However, voluntary movements usually have multiple sensory consequences. Tapping a tabletop, for example, creates visual, auditory, tactile, and proprioceptive feedback, which need to be integrated. In general, the nervous system maintains the perception of synchrony between the senses despite variations in the arrival times of sensory inputs to the brain (Fain, 2003). This mechanism is important presumably to determine whether the events are from single or multiple sources (Levitin et al., 2000). Therefore, for example, there is a tendency to perceive two sensory events as simultaneous if they are thought to originate from a common source (Stevenson et al., 2012; van Wassenhove et al., 2007; Zampini et al., 2003).

Very few studies have focused on timing perception in which a voluntary action has multiple sensory consequences. In one study, Parsons et al. (2013) assessed recalibration for the perceived timing of AV stimulus pairs preceded by voluntary button presses. They found that the predictable auditory stimulus was perceived as shifted in time, whereas the perceived timing of the unpredictable visual stimulus remained constant. The authors explain this finding with regard to the prior assumption that sensory consequences of actions should occur without a delay (Stetson et al., 2006) and that the perceptual system interprets events occurring at short delays after an action as the sensory consequences of that action (Eagleman and Holcombe, 2002). In a recent study, Desantis and Haggard (2016b) investigated the influence of action planning and prediction on AV temporal grouping. In the study, participants first learned associations between different simultaneous AV pairs to voluntary button presses or to visual cues. Therefore, both auditory and visual stimuli were predictable by either a movement or a sensory cue. Results showed increased tolerance to asynchronies for AV pairs when they followed previously associated actions. Moreover, they demonstrated that the perception of simultaneity for AV pairs depends on learned timing relations between the action and the outcome of that action. Another related study by Corveleyn et al. (2015) investigated mechanisms playing a role in sensory binding for action versus perception. Using a perceptual and a motor task, they assessed how judgments of relative timing regarding changes in the color and position of a visual target would differ when they were followed by a voluntary movement. Results indicate reduced temporal asynchrony between color and position changes in the target when they were temporally and spatially close to the movement. The researchers conclude that voluntary actions seem to facilitate binding of sensory events that they trigger, by influencing timing constraints inherent in the neural processing of sensory inputs, leading to a reduction in perceived asynchrony between events.

In both Desantis and Haggard (2016b) and Parsons et al. (2013), the focus was on the perceptual grouping of multisensory stimuli when they were triggered by a voluntary movement compared with when they occurred without movement. Similarly, in the Corveleyn et al. (2015) study, the interest was on the perception of changes in intrinsic and extrinsic properties of a target when it was followed by a movement compared with when it was only perceived. In other words, these studies focus more on the influence of voluntary movements on the perception of simultaneity for sensory events, as opposed to when these events occur externally. Therefore, the control conditions in these experiments consisted of passive viewing of the sensory stimuli, which made it possible to assess mere perceptual grouping effects. However, to investigate the effect of action-related predictive processes on the perceptual grouping of sensory inputs, the specific influence of the voluntary movement itself should be considered as well. Voluntary movements lead to both efferent and re-afferent feedback. On the other hand, sensory feedback that is externally triggered provides only re-afferent information (Weiskrantz et al., 1971).

In Study 1, the aim was to investigate how perception of simultaneity was maintained for the multisensory consequences of a voluntary movement. Specifically, the involvement of temporal contiguity and action-related predictive processing on the perception of simultaneity for multisensory stimuli were assessed. For this purpose, temporal relationship between the action and the multisensory feedback was varied to investigate how changes in temporal contiguity would influence perceived timing of these feedback. In a second experiment, the influence of action-related predictive processing on the perception of simultaneity for sensory inputs was addressed. In both experiments, participants were asked to initiate button presses at a time of their choice. The button press triggered the occurrence of a dot and a tone with a range of stimulus onset asynchronies (SOAs). The participants decided whether the dot and the tone were simultaneous or not. The stimulus pairs were presented either immediately following the button press or with one of two delays. Research on simultaneity perception suggests that there is a tolerance for how far two stimuli can be separated in time and still be perceived as simultaneous. This time window, known as the window of subjective simultaneity (WSS), has been found to be influenced by the assumption that both signals originate from a single source (the 'unity assumption'; Vatakis and Spence, 2007). In line with this, increased tolerance for asynchronies in AV stimuli was expected when they were contiguous with the action. To address the specific influence of voluntary movement, an externally controlled button was used in Study 1.2, which allowed for manipulating the influence of action-related predictive processing on AV simultaneity judgments (SJs). Increased tolerance to asynchronies was expected in the voluntary condition compared with the involuntary condition, as the participants would not be in control of the occurrence of AV stimulus pair. Support for this comes from studies showing less or no temporal binding to actions to their outcomes when the actions are not voluntary (Haggard et al., 2002; Tsakiris and Haggard, 2003). This study is the first to assess the influence of action-related predictive processing defined as the absence of intention on simultaneity perception for AV stimuli (representing multisensory consequences of an action).

3.2 Study 1.1

3.2.1 Methods

3.2.1.1 Participants

Twenty-four right-handed students (mean age 24.1±2.6, 16 females) from Philipps University Marburg took part in the experiment. Informed consent was obtained from all participants included in the study. They reported normal or corrected-to-normal vision and normal hearing. Right-handedness was confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971). The experiment was approved by the local ethics committee and performed in accordance with the Declaration of Helsinki. The participants were paid for their participation.

3.2.1.2 Apparatus

Visual stimuli were presented on a 24'' computer screen (1920 x 1200 pixels resolution, 60Hz frame refresh rate). Auditory stimuli were presented via headphones. Stimulus presentation was controlled by Octave and Psychtoolbox-3 (Brainard, 1997). A chin rest was used to stabilize the subject's head during the experiment. Button presses were made via a button pad using the participant's right hand. The button pad was covered with a black box to prevent participants from using visual cues. Responses were made on a keyboard ('V' for 'Yes', 'N' for 'No') using the left hand.

3.2.1.3 Stimuli and procedure

The visual stimulus was a black dot (1.5° visual angle, 0cd/m^2 luminance) at the center of the display against a neutral gray background (~89 cd/m^2 luminance). The auditory stimulus was a pure auditory tone burst with a frequency of 250Hz. To attenuate potential auditory cues arising from the button press, white noise was presented throughout the whole experiment. There were two within-subject factors: SOA and delay. Eleven SOAs between the auditory and visual stimuli were used: ±417.5, ±334, ±250.5, ±167, ±83.5, and 0ms. Negative SOAs indicate that the auditory stimulus was presented first, whereas positive SOAs indicate that the visual stimulus was presented first. The duration of the first stimulus (dot or tone) was 1000ms, and stimulus pairs always terminated at the same time.

Therefore, the actual duration of the lagging stimulus was smaller than 1000ms, depending on the SOA. Because we were interested in how movement influences the perception of synchrony, we instructed participants to use event onset times, rather than the offsets. Three delays were presented between the button press and the occurrence of the first stimulus: 0ms, 417.5ms, and 2500ms. A previous study by Haggard et al. (2002) suggested that binding of actions to their effects was stronger when the timing between the action and the consequence was around 250ms in comparison to 450 or 650ms, that is, when the stimulus was time contiguous with the action. Another study showed a decreasing tendency to perceive a stimulus as not representing the consequences of a voluntary action after a long delay (Eagleman and Holcombe, 2002; but see Humphreys and Buehner, 2010). We therefore used an intermediate delay of 417.5ms and a very long delay of 2500ms. The long delay was expected to serve as a condition in which the action and the effect was torn far apart in time, presumably leading to an impression that the effect did not originate from the action. Each SOA was repeated 10 times for each delay, for 330 trials. The trials were divided into two experimental runs. The combination of SOAs and delays were presented in random order with the restriction that both runs had the same number of delays and SOAs.

The experiment was conducted in a dimly lit room. Participants sat in front of the computer screen at a viewing distance of 54cm. They were instructed to place their right hand on a button pad, with their index finger on the button. Participants were instructed to perform button presses at a self-chosen time after a cue. The button press triggered the occurrence of the stimulus pair. The task was to judge whether the dot and the tone were simultaneous or not. Participants were also told that in some trials, there would be a delay between their button press and the occurrence of the stimulus. However, they were told that the task in these trials would remain the same: judging the simultaneity of the dot and the tone. To familiarize participants with the stimuli and the task, participants completed a block of 45 trials with smallest and largest SOAs and delay conditions (5 trials for each combination) with feedback before the start of the experiment. The practice trials were followed by the two experimental runs with a short break in between the runs. The whole procedure took 1.5 hours.

Each experimental trial started with a variable intertrial interval (ITI; 1000, 1500, 2000ms) during which a fixation cross (0.5 x 0.5cm) was presented. After the ITI, a black square (310 x 310pixels, 3.2° visual angle) surrounding the fixation cross was presented in the middle of the screen. This square served as a cue for participants to initiate their button press. The participants were instructed to wait for approximately 700ms after the appearance of the square, but they could choose to wait longer if they wanted. This was done to elicit a well-prepared, self-initiated button press rather than an automatic reflex to the cue (Rohde and Ernst, 2013). If the button was pressed too early, a ‘too early’ warning was presented, and the trial was repeated. After the button press, the multisensory stimulus was displayed following one of the three delays. The square remained on the screen during the presentation of the stimulus pair. After the offset of the stimulus pair and the square, a 500ms interval followed. Subsequently, the question ‘Simultaneous? Yes/No’ was presented on the screen. Participants used their middle and index fingers of their left hand for responding ‘Yes’ or ‘No’ respectively. They were given a maximum of 4000ms to respond after which the next trial followed. If they took longer than that, next trial followed. The sequence is shown diagrammatically in Figure 1.

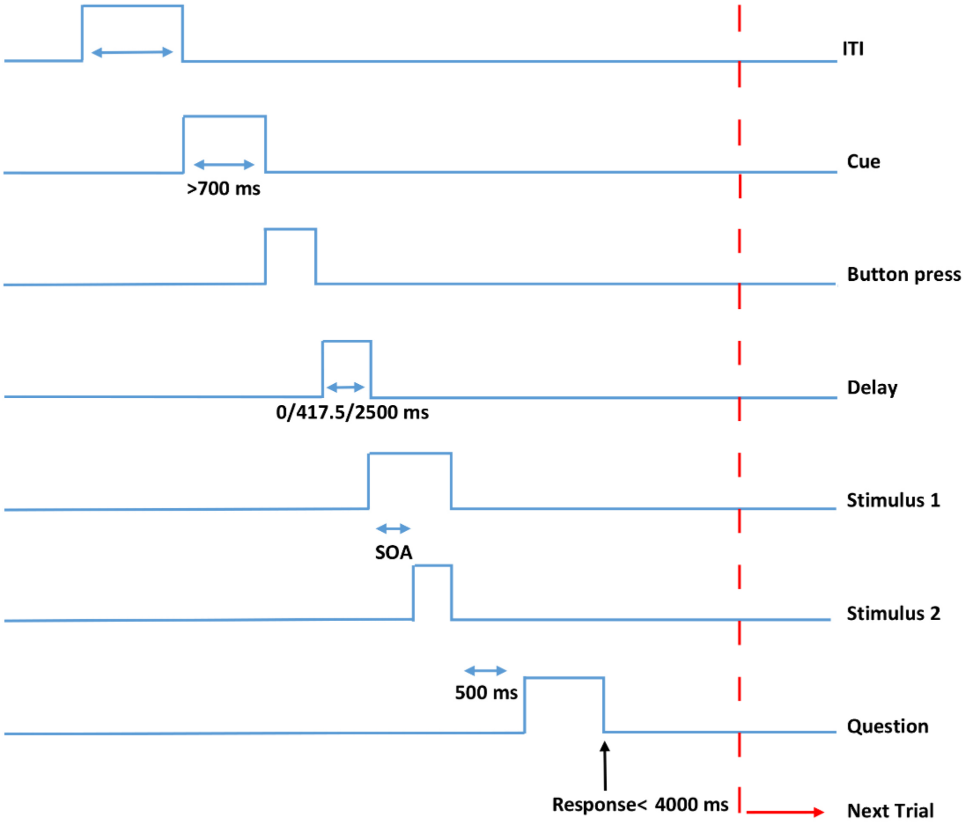


Figure 1. Timeline of an experimental trial in Study 1. After a variable ITI, a square cued participants to press a button at a time of their choice. Immediately or after a certain delay, a dot and a tone with variable SOAs (ranging from audition-leading 417.5ms to vision-leading 417.5ms) followed. The participants then judged whether the dot and the tone were simultaneous or not. ITI=intertrial interval; SOAs=stimulus onset asynchronies.

3.2.1.4 Data analysis

MATLAB 2012b (The Mathworks Inc., 2012) and psignifit toolbox version 2.5.6 for MATLAB (Fründ et al., 2011) were used for plotting SJs and fitting the data. SJs were plotted as a function of SOAs for each participant and delay. The data then were fitted with a two-criterion window model of the SJ task (Cravo et al., 2011; Rohde et al., 2014; Ulrich, 1987; Yarrow et al., 2013, 2011). This model generates a psychometric function that is constructed from the differences of two cumulative probability functions (each having a normal distribution) and has the following four parameters: two means (window limits) representing the positions of the decision criteria on the SOA axis for simultaneity, and two standard deviations (slopes) representing the sums of two sources of variability. The advantage of such a model is that it can account for asymmetries in perceiving simultaneity (Rohde et al., 2014; Yarrow et al., 2011). The values that fall between the decision criteria are considered simultaneous, defining the WSS. In the current experiment, the two sides of the psychometric function corresponded to the audition-leading and vision-leading sides, with positive values denoting that the dot came first.

Statistical analyses on the window limits and slopes was carried out using SPSS 21 (IBM Corp. Released 2012). Huynh–Feldt-corrected degrees of freedom were used in cases where sphericity was violated as indicated by the Mauchly's test of sphericity (Huynh and Feldt, 1976).

3.2.1.5 Deviance analysis

To test whether the participants were guessing or found the task difficult, the four-parameter model was tested against a simpler two-parameter model. This simpler model can capture participants who were guessing in which case their data would not vary systematically with SOA, or who were not given a sufficiently broad range of SOAs so that both transitions from synchrony to asynchrony would not be captured. The deviance for each model fit was estimated for each participant in each condition, and then the deviance difference (2 x difference in log likelihood) between the models was calculated. The difference in deviance from a simpler to a more complex model follows a chi-square distribution with degrees of freedom equal to the number of free parameters between the models (Yarrow, submitted). Participants were retained when this difference was significantly greater than the critical values for the chi-square distribution with 2 degrees of freedom (Yarrow et al., 2013; Yarrow, submitted). None of the participants was excluded on this basis.

3.2.2 Results

Statistical analyses were performed on the estimated window limits and slopes. For the statistical analyses on window limits, values on the audition-leading side of the curve were first sign-inverted to compare their distances from true simultaneity. A 2(Stimulus order: audition-leading vs. vision-leading) x 3(Temporal delays: 0 vs. 417.5 vs. 2500ms) repeated-measures analysis of variance (ANOVA) was conducted on the estimated window limits. There was a main effect of stimulus order, $F(1, 23) = 39.31$, $p < .001$, $\eta^2 = 0.35$. The window limits for audition-leading side (M across all delays = 178, SD = 16) were lower than the window limits for vision-leading side (M across all delays = 315, SD = 25; see Figure 2a). We also found a main effect of delay, $F(1.32,30.28) = 13.38$, $p < .001$, $\eta^2 = 0.11$. Bonferroni-corrected post hoc t tests showed significant differences between the 0ms (M = 301, SD = 27) and 417.5ms (M = 227, SD = 22) delays, $t(23) = 5.87$, $p < .001$, $d = 3.04$, and between 0 and 2500ms (M = 211, SD = 12) delays, $t(23) = 3.70$, $p = .001$, $d = 4.36$ (see Figure 2b).

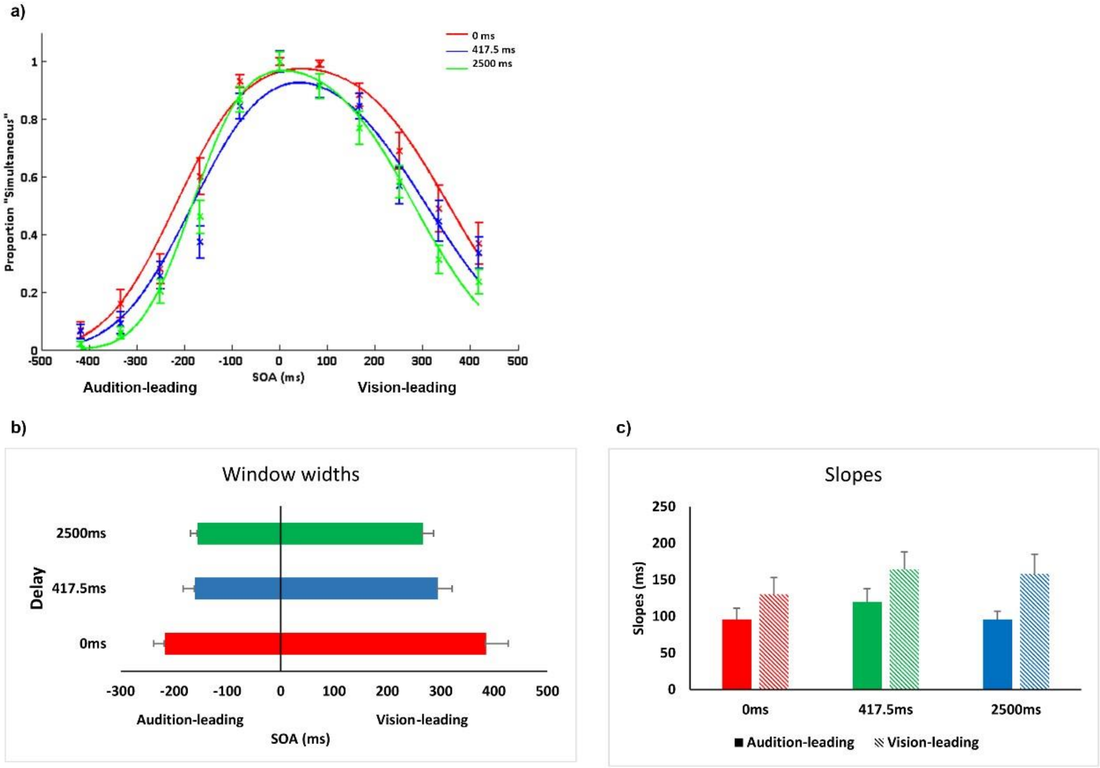


Figure 2. Results from Study 1.1. a) Proportion of 'simultaneous' responses as a function of SOAs for each delay, fitted to a two-criterion window model. Negative SOAs depict trials where the tone came first. Curves are normalized to the peak. The data depictions are provided for illustrative purposes only. Statistical analyses were based on individual data fits. b) Estimated WSS across all delays, derived from individual fits. c) Estimated

slopes across all delays, derived from individual fits. Error bars denote standard error of the mean. SOAs=stimulus onset asynchronies; WSS=window of subjective simultaneity.

A similar repeated-measures ANOVA conducted on the slopes showed a significant effect of stimulus order, F(1, 23) = 7.51, $p < .05$, $\eta^2 = 0.08$. Slopes for the audition-leading side (M = 102, SD = 13) were significantly steeper than the slopes for the vision-leading side (M = 148, SD = 19; Figure 2c). The slopes of the curves did not significantly differ across delays.

3.2.3 Preliminary Discussion

Participants were highly tolerant of asynchrony between a multisensory stimulus pair when it immediately followed the action. When the temporal interval between the action and the AV pair was increased, there was a greater sensitivity to asynchrony for these stimuli. However, this effect did not increase for the longest delay condition, suggesting that the effect might have saturated. When vision preceded audition, sensitivity to asynchronies was lower (as indicated by higher window limits and shallower psychometric functions) than when audition preceded vision. In other words, decision boundaries to judge the AV pair as simultaneous were higher on the vision-leading side than that of the audition-leading side. Such an asymmetry has been documented previously for AV SJs, in which the PSS was shifted toward a vision-leading stimulus and indicated that the perceived simultaneity is maximal if visual stimulus appears slightly before the auditory stimulus (Dixon and Spitz, 1980; Spence and Squire, 2003; Vatakis and Spence, 2006; Zampini et al., 2003).

Is the widened WSS related specifically to a voluntary movement or just to the occurrence of a stimulus pair immediately following a button press? To test this, we included an externally-generated movement condition in which the same task was performed, but with an automatically depressed button. With this condition, we aimed to assess the role of action-related predictions in judging simultaneity while maintaining comparable proprioceptive feedback for both conditions.

3.3 Study 1.2

3.3.1 Method

3.3.1.1 Participants

Twenty-four participants from Philipps University Marburg took part in the experiment (mean age = 24±3.13, 15 females). They were a different group from the participants in Study 1.1. Informed consent was obtained from all participants included in the study. They reported normal or corrected-to-normal vision and normal hearing. Right handedness was confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971). The experiment was approved by the local ethics committee and performed in accordance with the Declaration of Helsinki. The participants were paid for taking part in the experiment.

3.3.1.2 Apparatus

The setup was the same as in the first experiment, except that a custom-made button was used. This allowed for actively pulling the button down with an electromagnet (Intertec, ITS-LS2924B-D, 12V DC). Stroke length of the button was 5mm with a micro switch triggered within the last 0.2mm of movement. Both voluntary manual and externally activated button presses were recorded by the computer as a left click of a USB mouse. Therefore, jitter and delay of the button press did not depend on whether the condition was voluntary or externally-generated. For the voluntary movement, the initial force was 1.5Newton (N), as measured by a spring force gauge, slowly increasing to approximately 2.5N in the final position. In the externally-generated movement condition, the finger was initially pulled with approximately 1N, and the force increased to approximately 4N in the final position. The duration of the depression of the button press in the externally-generated condition was set to 300ms that was representative of the duration of the button press based on a previous piloting. The AV stimulus pair was presented only when the button was depressed completely, both for voluntary and externally-generated conditions. Participants wore soft foam earplugs to attenuate the sound of the ‘external’ button press. Moreover, white noise was presented to attenuate any sound, especially the one caused by the externally activated button. The participant’s right index finger was fixed to the button by a cotton bandage that was flexible enough not to cause discomfort. This was done to ensure that the finger would go along with the button in the externally-generated condition. The cotton bandage was present in both voluntary and externally-generated conditions.

3.3.1.3 Stimuli and procedure

The stimuli were identical to Study 1.1 with the following differences: The 2500ms delay condition in Study 1.1 was not found to be different than the intermediate delay condition. For that reason, we excluded the longest delay condition was excluded and an intermediate delay between 0 and 417.5ms delays was included. The following delays were used: 0, 167.7, and 417.5ms. The procedure was identical to Study 1.1, except for the following: In the voluntary condition, participants made button presses at a self-paced time, with the same timing (>= 700ms) criterion as in Study 1.1 following the start of the cue. In the externally-generated condition, the button was pulled down automatically by the computer after the appearance of the cue. The timing of the automatic button press was jittered across trials (700–1500ms). This was done to prevent participants from predicting the timing of the button press from the cue. The participants were presented with both voluntary and externally-generated conditions divided into 2 runs on 2 consecutive days. The order of voluntary and externally-generated conditions were counterbalanced across participants. The entire procedure took 1.5 hours.

3.3.1.4 Data analysis

The analysis was the same as in the previous experiment. One participant completed only the first half of the study, so the data from this participant was excluded. The data from the remaining 23 participants were analyzed (mean age = 23.57±3.34, 14 females). The data were plotted and fitted to the two-criterion model. Deviance analyses showed that three participants had one condition that did not conform to the chi-square distribution. All data from these participants were excluded from the final analyses.

3.3.2 Results

A 2(Movement type: voluntary vs. involuntary) x 2(Stimulus order: audition-leading vs. vision-leading) x 3(Temporal delays: 0 vs. 167.7 vs. 417.5ms) repeated-measures

ANOVA was conducted on the estimated window limits. There was no main effect of movement type, F(1, 19) = 3.50, p = .08. There was a main effect of stimulus order, F(1, 19) = 17.35, p < .01, $\eta^2 = 0.23$. Thus, previous results on asymmetrical window limits for simultaneity when vision led audition (M = 257, SD = 26) in comparison to when audition led vision (M = 159, SD = 15; Figure 3a and b) were replicated. There was also a main effect of delay, F(1.88, 35.68) = 34.75, p < .001, $\eta^2 = 0.14$. Bonferroni-corrected post hoc t tests showed that there was significant differences across all the delay conditions: between 0ms (M = 257, SD = 16) and 167.7ms (M = 205, SD = 21), t(19) = 5.88, p < .001, *d* = 3; between 167.7 and 417.5ms (M = 163, SD = 21), t(19) = 3.56, p = .002, *d* = 2.05; and between 0 and 417.5ms, t(19) = 7.25, p < .001, *d* = 5.31 (Figure 3c). A significant interaction between stimulus order and delay was also found, F(1.62, 30.71) = 8.07, p < .01, $\eta^2 = 0.02$. Bonferroni-corrected post hoc t tests showed that in the audition-leading side of the curve, the window limits were significantly higher for the 0ms (M = 192, SD = 90) compared with the 167.7ms (M = 157, SD = 78) delay, t(19) = 4.89, p < .001, *d* = .08; the 167.7ms compared with the 417.5ms (M = 86, SD = 89) delay, t(19) = 4.54, p < .001, *d* = 0.09; and the 0ms compared with the 417.5ms delay, t(19) = 9.73, p < .001, *d* = 1.67. For the vision-leading side, the window limits were significantly higher for the 0ms (M = 293, SD = 102) compared with the 167.7ms (M = 244, SD = 131), t(19) = 3.75, p = .001, *d* = 0.42; and the 0ms compared with the 417.5ms (M = 234, SD = 134), t(19) = 3.53, p = .002, *d* = 0.51.

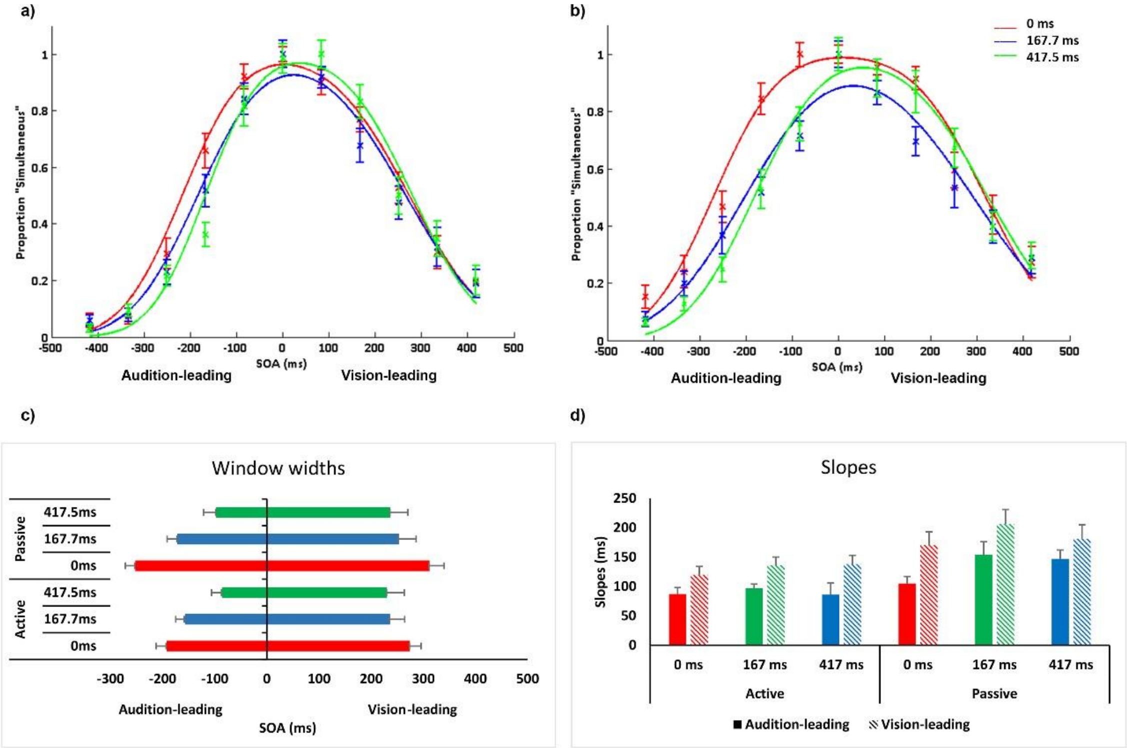


Figure 3. Results from Study 1.2. a) and b) Proportion of 'simultaneous' responses as a function of SOAs for each delay, fitted to a two-criterion window model, for voluntary and externally-generated conditions, respectively. Negative SOAs depict trials where the tone came first. Curves are normalized to the peak. The data depictions are provided for illustrative purposes only. Statistical analyses were based on individual data fits. c) Estimated WSS across all delays, collapsed across voluntary and externally-generated conditions, derived from individual fits. d) Estimated slopes across all delays, collapsed across voluntary and externally-generated conditions, derived from individual fits. Error bars denote standard error of the mean. SOAs=stimulus onset asynchronies; WSS=window of subjective simultaneity.

A similar repeated-measures ANOVA was conducted on the slopes. There was a main effect of movement, F(1, 19) = 30.78, p < .001, $\eta^2 = 0.09$ (Figure 3d). The slopes for the voluntary condition (M = 118, SD = 7) were significantly steeper the slopes for the self-generated condition (M = 160, SD = 11). There was also a main effect of delay, F(1.46, 27.76) = 4.51, p < .05, $\eta^2 = 0.03$. Bonferroni-corrected post hoc t tests showed that the slopes were significantly steeper for 0ms (M = 120, SD = 11) compared with the 167.7ms delay (M = 148, SD = 11), t(19) = 4.25, p < .001, *d* = 2.58, and the 0ms in comparison to the 417.5ms delay (M = 148, SD = 10), t(19) = 2.11, p = .049, *d* = 2.72. There was also a main effect of stimulus order, F(1, 19) = 7.28, p < .01, η^2 = 0.07. The slopes for the audition-leading side of the curve (M = 119, SD = 9) were significantly steeper than the slopes for the vision-leading side of the curve (M = 158, SD = 13), which was again a replication of the asymmetry.

3.3.3 Preliminary Discussion

In the second experiment, increased tolerance for AV asynchronies around the time of action was found, replicating our previous finding. This was also the case for the self-generated condition, suggesting that the contribution of action-related predictive mechanisms, which was expected to be much better for the voluntary condition, did not in fact have an effect on the tolerance for SOAs in simultaneity perception. Delaying the presentation of the stimulus pairs after the movement led to decreased tolerance for asynchronies both for voluntary and externally-generated movements. The slopes of the psychometric functions were significantly steeper for the voluntary in comparison to the externally-generated condition. This finding suggests that the participants' responses in the externally-generated condition were more variable. Moreover, the difference in slopes with the inclusion of delays suggests that overall SJs had more variance in the presence of delays. The finding of asymmetrical window limits and slopes for the audition- and vision-leading sides of the SJ curve were replicated.

3.4 General Discussion

In the present experiments, we investigated the perception of simultaneity for multisensory stimuli triggered by voluntary or involuntary movements and compared SJs when the timing between action and the feedback was and was not contiguous. The WSS widened when stimuli were contiguous with the action. Introducing a delay between the action and the AV feedback increased sensitivity for AV asynchrony. In other words, the decision boundaries for judging the stimuli as simultaneous were significantly wider when AV stimuli immediately followed the button press than when a delay was added. Introducing a delay of 2500ms, which eliminated contiguity for the action-effect relationship, produced data that were not different from introducing 417.5ms delay, suggesting that 417.5ms was enough to break contiguity. The similarity between the voluntary and externally-generated conditions suggests that perceiving simultaneity between the AV stimuli was not affected by action-related predictive mechanisms. However, the psychometric slopes were steeper when participants pressed the button voluntarily as compared to when the movement was externally triggered. We now discuss these findings in detail.

There are a number of possible explanations with regard to our finding of increased tolerance of SOA in the perception of simultaneity when the action was time contiguous with AV feedback: First, the participants could have become more likely to perceive both components as due to their action, and therefore should be linked, which then might have led to a shift in the perceived timing of sensory stimuli toward the action. Second, time could be perceived as slowed around the point where the action was executed, and therefore it was harder to make any kind of temporal judgment. The two explanations presumably lead to intentional binding of an action to its consequences. However, each explanation underlies a different type of processing of time around the occurrence of an action (Haggard et al., 2002; Morrone et al., 2005). The first explanation is related to timing shifts toward an action. According to this hypothesis, the subjective timing of anticipated action-effect intervals is shifted backward in time toward the action, which leads to perceived shortening of action-effect intervals (Wenke and Haggard, 2009). In both Study 1.1 and 1.2, the WSS were found to be increased for the AV stimulus pair when it immediately followed the movement, suggesting a possible time shift for the second sensory stimulus relative to the first sensory stimulus that was presented immediately following the action. An alternative explanation could be the compression of perceptual time around the point of an action (Morrone et al., 2005; Wenke and Haggard, 2009). Accordingly, operant movements such as voluntary actions cause compression of time around the movement, which is thought to stem from a slowed internal clock speed during the movement. This leads to compressed intervals between the action and the effect. In this respect, the widened WSS around the time of the action in the current studies might correspond to perceptual time slowing down and events seeming to be closer together in time than they normally are. Although the finding of poor temporal discrimination around a voluntary movement cannot be directly attributed to time shift or compression, it suggests that participants are highly tolerant of asynchrony between a multisensory stimulus pair when they immediately followed the action. Such tolerance might facilitate perception of synchrony between multisensory action outcomes. The findings of the current studies clearly highlight the differential contribution of voluntary movements in perceiving multisensory inputs and is in line with the literature on the differential processing of sensory information in relation to voluntary movements (Corveleyn et al., 2015; Desantis and Haggard, 2016b; Parsons et al., 2013). As in these studies, current findings similarly indicate a reduction of temporal asynchrony between sensory events attributed to an action. In addition, including delays between a movement and its consequences resulted in a similar increase in perceiving asynchronies. These results in general underlie the complex relationship between action and perception, adapted to the demands of the world we are interacting with. Supporting this view comes from research on peripersonal space (PPS). PPS, defined as the region around the body, is important for survival as harmful stimulus poses a more likely threat when it is near the body, and our interactions with the external world usually occurs within this space (Brozzoli et al., 2011; Graziano and Cooke, 2006). When considered in the context of the current studies, PPS provides an important clue to the mechanisms underlying the prioritized processing of sensory inputs near us or those inputs resulting from our own action. A recent study by Noel et al. (2016) addressed this issue by investigating how perception of simultaneity for an AV event is influenced by whether they were within or outside the person’s PPS. By manipulating the distance of AV events to the body (inside or outside PPS), they found significantly higher SJs when the stimuli were within the PPS. The study provides additional support to the finding that a more liberal binding criteria within the context of PPS is advantageous for an efficient processing of sensory information being in close proximity to the body, where interaction with the external world is more likely (Brozzoli et al., 2012; Graziano and Cooke, 2006; Rizzolatti et al., 1997). Current findings regarding wider WSSs around a movement are in line with Noel et al. (2016), as both studies support flexible criteria for binding sensory information when interacting with and reacting to the world.

Despite the finding on timing distortions linked to voluntary movements, larger binding windows for AV stimulus pairs were found around the time of externally-generated movements as well. An alternative explanation of these findings therefore involves the assumed causal relations between events. Following from a Bayesian view, there is a general prior assumption that causally related events are more likely to occur close in time and space (Eagleman and Holcombe, 2002; Hume, 1748). For example, Buehner (2012) demonstrated that predictive relations were constructed not only for voluntary movements or intentional agents but also when a machine caused the event. However, in contrast, there is also evidence that involuntary movements lead to less binding than voluntary movements (Tsakiris and Haggard, 2003; Wohlschläger et al., 2003). There are studies suggesting that both intentionality of the movement as well as causal relations between the events are important (Cravo et al., 2011, 2009; Moore and Haggard, 2008). Current results are more in line with this view as increased WSS for AV pairs were both present for voluntary and externally-generated conditions, suggesting that contiguity between the button press and the AV stimuli led to an increased distortion of time for these events, both when the participants were voluntarily initiating them as well as when they were mechanically initiated. This view still predicts attraction between causally related events outside of one's own control (Eagleman and Holcombe, 2002). In both voluntary and externally-generated conditions, a causal relationship between the button press and the appearance of an AV pair was present. Nevertheless, an interesting finding emerged in the form of steeper slopes for the voluntary condition, suggesting that the participants were more precise in their judgments when they were initiating the button press. This points to the differential processing for the consequences of voluntary movements and is in line with the finding that people are more confident about events that they caused (Stetson et al., 2006). Therefore, when the participants voluntarily initiated the movement, they were more confident that the AV feedback was simultaneous than when the button press was externally initiated.

A possible implication for the increased WSS in our study is related to the assumption of unity in perceiving synchrony. It has been claimed that intentional binding might contribute to the assumption of unity, which is a prerequisite for integrating sensory signals (Rohde et al., 2014; Rohde and Ernst, 2013). For two events to be bound, they should fall within a window of integration (Bresciani et al., 2005; Shams et al., 2000). Following from this, it could be argued that in the current study this prior assumption was present, and that the perception of simultaneity was maintained over a range of asynchronies for stimuli that were causally linked to a button press be it a voluntary or an externally-generated event.

It should be pointed out that in the current studies, self-generated stimuli were predictable in time, while the comparison stimuli occurred at unpredictable times. This could be viewed as a plausible and sufficient comparison condition considering the real-world situations where externally-generated movements are often unpredictable. However, in their review, Hughes et al. (2012) point to mechanisms other than motor prediction that might influence the sensory processing of action effects. Among them is temporal prediction, which is defined as ‘‘the ability to predict the point in time at which a sensory event will occur’’ (p. 135). In this sense, a stimulus can be predictable in time when it follows a voluntary or an externally-generated movement, so long as it occurs at a specified point in time after the movement. In the current studies, window limits were similar for the voluntary and externally-generated conditions, but the judgments were noisier in the externally-generated condition (shallower slopes). This increase in noise could reflect the fact that stimuli were less precisely predictable in the externally-generated condition than they were following a voluntary button press.

Research on multisensory binding consistently shows that the brain adapts to the prolonged exposure of asynchronous multisensory stimuli to compensate for environmental influences as well as differences in the speed of neural processing (Fujisaki et al., 2004; Vroomen et al., 2004). Recently, it has been demonstrated that adaptation can take place in a rapid fashion, even without consciously attending to the temporal relations between sensory inputs (Harvey et al., 2014; Van der Burg et al., 2015, 2013; Van der Burg and Goodbourn, 2015). Therefore, we assessed whether current results could be explained by rapid recalibration in post hoc analyses. There was no indication of such an effect and therefore the possible impact of recalibration in explaining current results were ruled out. However, the effect of rapid recalibration would be an interesting topic for future studies.

It should be noted that although duration of a stimulus is not indicated as a significant factor affecting synchrony perception (Vatakis and Spence, 2006), differences in the duration of auditory and visual stimuli have been found to influence judgments of synchrony (Kuling et al., 2012). This effect is not seen when the durations of both stimuli were matched. In the current studies, the durations of the visual and auditory stimuli changed, so as to encourage participants to attend to the onsets, and not offsets in judging simultaneity. As a result, depending on the SOA, different durations of auditory and visual stimuli were presented. Although it has been shown that increases in the absolute duration of multisensory stimuli lead to decreases in inter-subject variability of PSS (Boenke et al., 2009; Kuling et al., 2012), future studies are needed to address the complementary effects of duration on the perception of synchrony.

Another point concerning the length of stimuli is the possibility that participants in the current studies made use of durations rather than onsets in judging simultaneity. There is evidence that intervals with an auditory onset are perceived to be longer than intervals with an auditory offset (Grondin and Rousseau, 1991; Ortega et al., 2014; Zampini et al., 2005a, 2005b). However, this effect is found to occur if the onsets and offsets of the auditory and visual stimuli are in close temporal proximity to each other (Chen and Yeh, 2009; Klink et al., 2011; Romei et al., 2011). In the present studies, although stimulus offsets were always the same, the onsets were mostly incongruent. In this sense, the impact of auditory stimulus on judging simultaneity might not be an explanation for current findings as incongruencies were present more than congruencies. In addition, a recent study by Linares and Holcombe (2014) regarding the perception of latency for AV stimuli indicates that the asymmetric criterion present in judging simultaneity is not present for duration judgments. Considering this and other results on the auditory capture of duration, it could be argued that if the decisions were based more on duration rather than on simultaneity, window widths and slopes for audition- and vision-leading sides would be similar. Instead, significant differences regarding window widths and slopes of the audition- and vision-leading sides were observed, suggesting simultaneity to be more relevant for the participants in performing the task.

In conclusion, Study 1.1 and 1.2 show increased tolerance for asynchronies between AV stimuli around the time of an action that might facilitate binding of sensory signals and compensate for incongruent timing between the senses. A similar pattern emerged for externally-generated movements, underlying the importance of causal relations between events. Nevertheless, a unique contribution of action-related predictions in perceiving simultaneity for events emerged with increased precision for judging simultaneity when they follow voluntary movements.

4 STUDY 2: NEURAL CORRELATES OF MULTISENSORY ACTION OUTCOMES

The content of Study 2 has been published as:

Straube, B., van Kemenade, B.M., Arikan, B.E., Fiehler, K., Leube, D.T., Harris, L.R., Kircher, T. (2017). Predicting the Multisensory Consequences of One's Own Action: BOLD Suppression in Auditory and Visual Cortices. PLoS One 12, e0169131. doi:10.1371/journal.pone.0169131.

4.1 Background

It has been established that the sensory consequences of voluntary actions are perceived differently than externally-generated sensory inputs. One observed phenomenon for this differential type of processing is the reduced sensation for the outcomes of voluntary movements, which is known as sensory suppression (Bays et al., 2005; Blakemore et al., 1998; Desantis et al., 2012; Shergill et al., 2013). Suppression is thought to be useful for the efficient processing of unexpected and salient stimuli, and inferring agency over events (Blakemore and Frith, 2003). Recent theories of motor control explain this phenomenon within the forward model framework, where an internal model anticipates the sensory outcomes of voluntary actions, and monitors whether predicted outcomes match actual ones (Blakemore et al., 1999, 1998; Wolpert and Ghahramani, 2000). Efference copies are then thought to modulate the neural processing in the corresponding sensory cortex, resulting in reduced sensation for the outcomes of voluntary movements (Pynn and DeSouza, 2013). Sensory suppression has been studied extensively for somatosensory, auditory and visual domains, both on a behavioral (Bays et al., 2006; Cardoso-Leite et al., 2010; Roussel et al., 2013; Sato, 2008) and neural level (Blakemore et al., 2001; Blakemore et al., 1998; Hughes and Waszak, 2011; Lange, 2011; Roussel et al., 2014; Shergill et al., 2013). As regards neural correlates, voluntary movements have been found to recruit the dorsolateral prefrontal cortex (DLPFC), cingulate motor areas/ACC and SMA during planning, initiation and execution compared with externally-generated movements

(Cunnington et al., 2005, 2002; Deiber et al., 1999; Jenkins et al., 2000b; Lau et al., 2004; Mueller et al., 2007; Weiller et al., 1996). Candidate areas proposed to be involved in the generation and updating of efferent signals include the SMA (Haggard andWhitford, 2004) and the cerebellum (Blakemore et al., 2001; Blakemore et al., 1998; Knolle et al., 2012; Wolpert et al., 1998), whereas inferior parietal regions have been implicated in visuo-motor integration (Christensen et al., 2014; Schnell et al., 2007) and processing of action outcome discrepancies (Blakemore and Sirigu, 2003; Farrer et al., 2008). Moreover, studies have demonstrated that the behavioral and neural indices of sensory suppression decreases with spatiotemporal discrepancies between the predicted and the actual sensory outcome, or when the outcome is incongruent with predictions (Bays et al., 2005; Benazet et al., 2016; Blakemore et al., 1998; Cardoso-Leite et al., 2010).

These studies, along with others investigating action-related predictive processes have mostly focused on unimodal action outcomes. However, voluntary actions in the real world often lead to multisensory outcomes. Research on multisensory processing points to the facilitatory effect of a certain stimulus modality on another modality when they are spatially and/or temporally in synchrony (Diederich and Colonius, 2004; Meredith et al., 1987; Stein, 2012). On the other hand, there is evidence that one modality can have an inhibitory effect on another modality (Colavita, 1974; Meredith, 2002; Morein-Zamir et al., 2003; Sinnett et al., 2008; Wang et al., 2012). In the case of action-related effects, few studies exist which address multisensory influences in the processing of action outcomes in the behavioral domain (Desantis et al., 2014; Desantis and Haggard, 2016b; Farrer et al., 2013; Kawabe et al., 2013; van Kemenade et al., 2016). By demonstrating that multisensory inputs associated with voluntary actions modulate time perception for these action outcomes compared with unimodal inputs triggered by similar actions, these studies underline the influence of multisensory processing on action outcome processing. However, despite recent interest in exploring multisensory action outcomes, very few studies have been conducted on the issue (Desantis and Haggard, 2016b; Parsons et al., 2013; van Kemenade et al., 2016). Moreover, the neural basis of perceiving multisensory action outcomes has so far been overlooked. The aim of Study 2 in the present dissertation was to investigate neural correlates of perceiving unimodal vs. bimodal action outcomes in comparison with when these sensory inputs are not the result of an action, and just passively perceived. To this end, participants were asked to perform voluntary button presses triggering either unimodal auditory or visual vs. bimodal audiovisual outcomes. Delays between the button press and the sensory outcome were introduced, and the participants were asked to detect whether there was a delay between the button press and the outcome of a certain modality. With this design, the aim was to assess how action outcomes are perceived as opposed to passive viewing of similar sensory inputs, and how temporal discrepancies between the action and the outcome affect perceptual judgments. It was expected that delay detection would be higher for multisensory action outcomes compared with unimodal sensory stimuli, because additional modality would provide extra timing information about the action outcome. It was also expected that voluntary movements would lead to suppressed BOLD activity in sensory areas. Moreover, BOLD suppression effects would be present both when the action would lead to unimodal and bimodal outcomes, as both outcomes are equally likely. BOLD activity related to the detection of delays (subjective delay detection) was examined in order to address differences in brain areas when an action outcome was perceived as not delayed as opposed to when a delay was detected. It was also assumed that subjective delay detection-related BOLD activity would be influenced by whether the sensory outcome was unimodal or bimodal. Finally, possible task-related effects were also investigated in order to address differences in performing auditory vs. visual delay detection task, as it has been previously found that temporal perception might differ with regard to whether the target stimulus is auditory or visual (Repp and Penel, 2002).

4.2 Materials and Methods

4.2.1 Participants

21 healthy, right-handed participants confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971) with normal or corrected-to-normal vision took part in the experiment (13 females, age range 19±30, mean age 24.9 years). One participant had to be excluded from the fMRI analysis because of excessive movement, resulting in a sample of twenty participants (12 females, age range 19±30, mean age = 25.1 years). The study was approved by the local ethics committee and in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

4.2.2 Stimuli and Procedure

During fMRI data acquisition participants wore headphones (MR-Confon Optimel, Magdeburg, Germany) through which auditory stimuli were delivered in the form of a pure-tone 250Hz beep. The visual stimulus was a black dot (1.5° visual angle), presented centrally in front of a medium grey background via a computer screen (60Hz screen refresh rate) positioned behind the scanner, and viewed via an angled mirror inside the MRI scanner. The duration of unimodal visual and auditory, as well as bimodal audiovisual stimuli was 1000ms. Stimuli were presented using Octave and Psychtoolbox-3 (Brainard, 1997).

An event-related fMRI design was used. The experimental paradigm used in Study 2 was adapted from a previous study (van Kemenade et al., 2016). However, due to technical reasons an externally-controlled button could not be included in the present study. Instead, a passive condition has been utilized whereby similar sensory stimuli triggered by button presses were shown after a cue. Participants were instructed to place index finger of their right hand on a button pad fixed to their leg via straps. Using the button pad, they were asked to perform button presses with their right index finger, which would elicit the appearance of either a dot on the screen, or a tone, or both. The stimuli were presented either at the time of the button press, or with a variable delay (0, 83, 167, 250, 334, 417ms, determined based on the screen refresh rate). In bimodal trials, delays were always of the same duration for both modalities. The task of the participants was to detect whether there was a delay between the button press and the accompanying stimuli of a certain modality. In other words, participants had to report delays in one modality in each trial, referred to as task modality. Thus, in bimodal trials participants only had to report whether they detected a delay between the button press and the visual or the auditory stimulus. In the passive condition, they were instructed to perform no button presses. Instead, they were asked to attend to the sensory stimuli presented, and to report whether there was one or two sensory stimuli. This control condition was selected for two reasons. First, with this condition, the participant had to attend to sensory stimuli, similar to that during the voluntary action condition. Second, the simplicity of the task did not require for more attention, making it unlikely that the expected suppression effects in the voluntary condition were confounded by increased task demand in the passive condition.

The experiment consisted of 5 blocks, in which voluntary conditions with different task modalities, along with one passive mini-block were presented in alternating order (visual-auditory-passive-visual-auditory, counterbalanced across participants). At the start of each mini-block, the task to be performed was presented (auditory, visual or passive). Each block comprised 60 trials in total, with 12 trials per mini-block. Unimodal and bimodal trials were randomly presented within each mini-block. The fMRI experiment comprised 300 trials in total: there were 10 trials for each delay per condition, leading to 60 voluntary unimodal visual trials ($Vol_{Uni}Vis$), 60 voluntary unimodal auditory trials ($Vol_{Uni}Aud$), 60 voluntary bimodal visual trials ($Vol_{Bi}Vis$) and 60 bimodal auditory trials ($Vol_{Bi}Aud$). Furthermore, unimodal and bimodal passive control conditions were presented: 20 visual unimodal ($Pas_{Uni}Vis$), 20 auditory unimodal ($Pas_{Uni}Aud$) and 20 bimodal ($Pas_{Bi}AV$).

Each experimental trial began with a fixation cross having variable inter-trial interval (1000-1500-2000ms). Subsequently, a square (3.2 degrees visual angle) surrounding the fixation cross appeared in the middle of the screen, comprising the cue. In the voluntary condition, the participants were instructed to perform button presses at their own pace in a fixed time window up to 4000ms after the cue onset. In this respect, they had some freedom in when to initiate the movement. This was done to encourage a self-initiated button press rather than an automatic reflex to the cue (Rohde and Ernst, 2013). The button press triggered either a unimodal or a bimodal stimulus pair after one of the six delays. The visual stimulus appeared at the location of the fixation cross, thus obscuring it. For unimodal auditory trials the fixation cross remained visible during the presentation of the tone. The cue and stimuli disappeared at the same time. Subsequent to the offset of the stimuli and cue, there was a variable interval with the fixation cross before the question `Delay? Yes/No' was presented on the screen, after a fixed period of six seconds after cue onset. They answered `Yes, there was a delay' by pressing a button with their left middle finger, or `No, there was no delay' by pressing a button with their left index finger. The left index and middle fingers were placed on two buttons of a separate button pad fixed to the left leg. In the passive condition, participants were instructed not to perform any button presses, but to just observe and listen to the presented stimuli after the cue. In these trials, the stimuli were presented automatically after a variable delay (500±3500ms) followed by a fixation cross.

The time from the start of the cue to the offset of the stimulus presentation was also 6000ms. After that, participants had to judge whether one or two stimuli had been presented, by pressing with their left middle finger for ‘Yes, there were two stimuli’, or left index finger for ‘No, there was only one stimulus’ to the question ‘Two stimuli? Yes/no’. The participants were given up to 2500ms for their answer. In addition, they were instructed to be as accurate as possible, but were not required to be as fast as possible. After the response, the next trial began. Missing trials in which no responses were registered were not repeated to maintain a fixed data acquisition procedure for all experimental runs and participants. Experimental trials regarding voluntary and passive conditions were depicted in Figure 4.

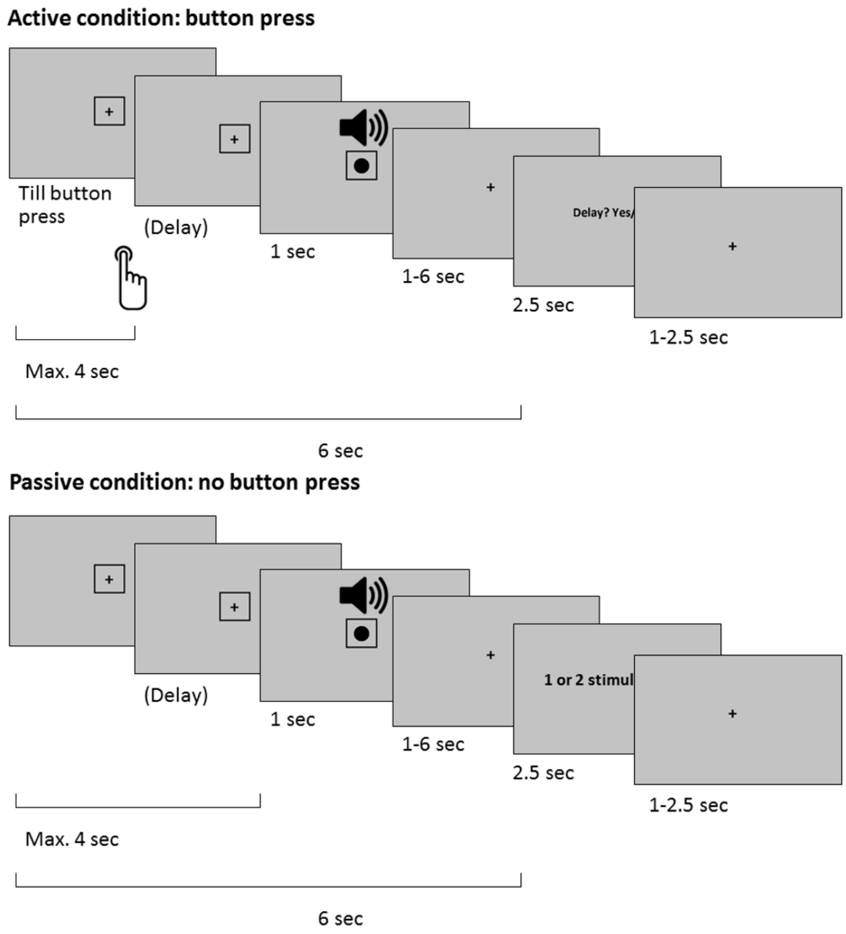


Figure 4. An example of a bimodal trial. In the voluntary condition (top) participants pressed the button at a time of their preference (max. 4000ms) after the appearance of the cue. After a variable delay, unimodal or bimodal stimuli were presented. Participants had to report whether there was a delay between their button press and the stimulus of the task modality. In the passive condition (bottom), an identical trial structure was used. However, no button press was performed, and the participants had to report whether they perceived one or two stimuli.

Approximately a week prior to the fMRI experiment, participants familiarized themselves with the task in a behavioral training outside the scanner. In the behavioral training, they initially practiced the button presses and with different sensory outcomes that could be initiated by the button presses. They then familiarized themselves with the delays, first with only 0 and the 417ms delays. They were also presented with the passive condition. Subsequently, they completed one run just as in the fMRI experiment, receiving feedback about their performance at the end of each trial. This was followed by two more runs, this time without feedback. Only those subjects having a performance of higher than 50% correct detection were invited to the fMRI experiment, as this was necessary to distinguish detection-related processes. All 21 participants met this criterion.

4.3 Data Analysis

4.3.1 Behavioral data analysis

Proportion of delay responses across each task and modality were calculated. In addition, average delay for detected and undetected trials were assessed for each condition. Statistical analyses were conducted on proportion of delay responses as well as average delay per condition. Button press latencies across conditions were extracted, and used to assess possible correlations between performance and movement initiation. Analyses were conducted on proportion delay responses and delays per condition. When necessary, Bonferroni corrected t tests were conducted for post hoc analyses.

4.3.2 fMRI data acquisition and analysis

MRI data were collected using a Siemens 3 Tesla MR Magnetom Trio Trim scanner. A total of 396 transversal functional images were acquired during each experimental run (echo-planar images, 64 x 64 matrix; 34 slices descending; field of view [FoV] = 230mm; repetition time [TR] = 1650ms; echo time [TE] = 30ms; flip angle = 70 °; slice thickness = 4.0mm, gap size: 15%, and voxel resolution = 3 x 3 x 4.6mm) covering the whole brain.

Preprocessing and subsequent analyses were performed using Statistical Parametric Mapping (SPM12; www.fil.ion.ucl.ac.uk) implemented in MATLAB 7.9 (Mathworks, Sherborn, Massachusetts). Preprocessing was comprised of standard realignment, coregistration between structural and functional scans, segmentation, normalisation (Montreal Neurological Institute [MNI] template 2 x 2 x 2mm) and smoothing (8mm).

Single subject analyses were conducted using a high-pass filter with a cut-off period of 128 seconds. Realignment parameters were modelled as regressors of no interest to account for movement-related artifacts. Two analyses were performed. In the first analysis, hemodynamic responses triggered by visual, auditory or bimodal stimuli during each condition ($Vol_{Uni}Vis$, $Vol_{Uni}Aud$, $Vol_{Bi}Vis$, $Vol_{Bi}Aud$, $Pas_{Uni}Vis$, $Pas_{Uni}Aud$, $Pas_{Uni}AV$) was modeled with a canonical HRF. In the second analysis, voluntary trials were grouped according to whether a delay was detected or not (subjective delay detection: detected and undetected). Button presses were also included as a condition of no interest. Parameter estimates (beta values) and t-statistic images were calculated for each subject.

On the second level, two random effects analyses were performed. In the first analysis, parameter estimates of the seven conditions ($Vol_{Uni}Vis$, $Vol_{Uni}Aud$, $Vol_{Bi}Vis$, $Vol_{Bi}Aud$, $Pas_{Uni}Vis$, $Pas_{Uni}Aud$, $Pas_{Uni}AV$) were added into flexible factorial model.

Expected effects and corresponding contrasts of interest were a) BOLD suppression for voluntary movements, by contrasting each control condition with the respective voluntary condition ($Pas_{Uni}Vis > Vol_{Uni}Vis$, $Pas_{Uni}Aud > Vol_{Uni}Aud$, $Pas_{Uni}AV > Vol_{Bi}Vis$, $Pas_{Uni}AV > Vol_{Bi}Aud$), b) task and modality-independent BOLD suppression, by conjunction analyses [$(Pas_{Uni}Vis > Vol_{Uni}Vis) \cap (Pas_{Uni}Aud > Vol_{Uni}Aud) \cap (Pas_{Uni}AV > Vol_{Bi}Vis) \cap (Pas_{Uni}AV > Vol_{Bi}Aud)$], c) differential processing of voluntary movements by contrasting voluntary with passive trials [$(Vol_{Uni}Vis + Vol_{Uni}Aud + Vol_{Bi}Vis + Vol_{Bi}Aud) > (Pas_{Uni}Vis + Pas_{Uni}Aud + Pas_{Uni}AV)$]. In the second analysis, parameter estimates for detected and undetected trials (detected vs. undetected) were entered into a flexible factorial design. Three subjects were excluded from this analysis due to insufficient number of trials per experimental run, resulting in seventeen participants (10 females, age range 19±30, mean age = 25 years). Contrasts of interests for this analysis were a) detected > undetected trials to assess whether BOLD activity differs with the detection of delays, b) detected > undetected using an inclusive mask to cover sensory brain regions found in the conjunction analysis, in order to explore possible BOLD suppression effects for undetected trials. Furthermore, possible interactions between detection and modality were also assessed.

Separate analyses were conducted to assess the potential influence of button press on findings. Accordingly, time during button press was not modelled (as a condition of no interest) in the first and the second analysis. Contrasts of interest were the same as in the first and second analyses.

To correct for multiple comparisons, family-wise error correction (FWE) correction at $p < 0.05$ was implemented. In order to avoid Type II error, the results were additionally assessed using $p < 0.001$ uncorrected, with a cluster extent of 50 contiguous resampled voxels. This is above the cluster threshold calculated by Monte Carlo simulations, which resulted in a minimum cluster size of 47 resampled voxels to achieve correction for multiple comparisons at $p < 0.05$, assuming an individual voxel type I error of $p = 0.001$ (Slotnick et al., 2003). AAL toolbox (Tzourio-Mazoyer et al., 2002) and the probabilistic cytoarchitectonic maps (Eickhoff et al., 2005) were used to label significant activations, based on peak activation voxels.

4.4 Results

4.4.1 Behavioral results

A 2(Modality: unimodal vs. bimodal) x 2(Task: visual vs. auditory) repeated measures ANOVA was conducted on proportion delay responses. There was a main effect of modality and task; $F(1,19) = 6.809$, $p = 0.017$, $\eta^2p = 0.264$, and $F(1,19) = 9.541$, $p = 0.006$, $\eta^2p = 0.334$, respectively (see Figure 5). No interaction effect was found; $F(1,19) = 2.861$, $p = 0.107$, $\eta^2p = 0.131$.

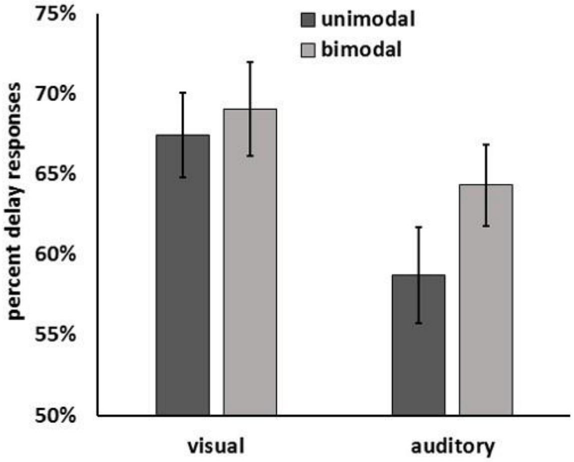


Figure 5. Proportion of delay detection in the voluntary condition as a function of task and modality. In both tasks, bimodal trials showed more delay responses than unimodal trials. Error bars denote standard error of the mean.

A repeated measures 2(Modality: unimodal vs. bimodal) x 2(Task: visual vs. auditory) ANOVA on button press latencies showed no significant differences across conditions. Additional correlation analyses revealed no significant correlation between button press latencies and performance in the task. Latency of the button press as a potential confounding factor was therefore ruled out.

Finally, performances in the passive task were calculated. The overall performances for the passive task suggested ceiling effects as indicated by extremely high accuracy rates, Pas_{Uni}Vis mean = 98.33%, SD = 4.36; Pas_{Uni}Aud mean = 98.75%, SD = 3.05; Pas_{Bi}AV mean = 97.91%, SD = 3.70. There were no significant differences in the performances across passive tasks ($p > 0.49$).

4.4.2 fMRI results

Passive > voluntary contrast across conditions (Pas_{Uni}Vis > Vol_{Uni}Vis, Pas_{Uni}Aud > Vol_{Uni}Aud, Pas_{Uni}AV > Vol_{Bi}Vis, Pas_{Uni}AV > Vol_{Bi}Aud) revealed significantly reduced BOLD responses in bilateral posterior occipital cortices, bilateral temporal cortices and the left motor cortex. Conjunction analyses across these contrasts [(Pas_{Uni}Vis > Vol_{Uni}Vis) ∩ (Pas_{Uni}Aud > Vol_{Uni}Aud) ∩ (Pas_{Uni}AV > Vol_{Bi}Vis) ∩ (Pas_{Uni}AV > Vol_{Bi}Aud)] suggest that BOLD suppression effects were overall independent of task or modality (see Table I and Figure 6). Voluntary > passive contrast [(Vol_{Uni}Vis + Vol_{Uni}Aud + Vol_{Bi}Vis + Vol_{Bi}Aud) > (Pas_{Uni}Vis + Pas_{Uni}Aud + Pas_{Uni}AV)] revealed significant differences in right pre-/postcentral gyrus (MNI: x, y, z = 38 -22 54, T = 9.72, $k_E = 796$, $p_{\text{FWE}} < 0.05$), left medial occipital lobe (MNI: x, y, z = -4 -86 -8, T=7.91, k_E=2742, $p_{\text{FWE}} < 0.05$), lingual gyrus/precuneus (MNI: x, y, z = 2 -54 2, T = 5.29, $k_E = 36$, $p_{\text{FWE}} < 0.05$) and left hippocampus (MNI: x, y, z = -26 -36 10, T = 5.13, $k_E = 8$, $p_{\text{FWE}} < 0.05$).

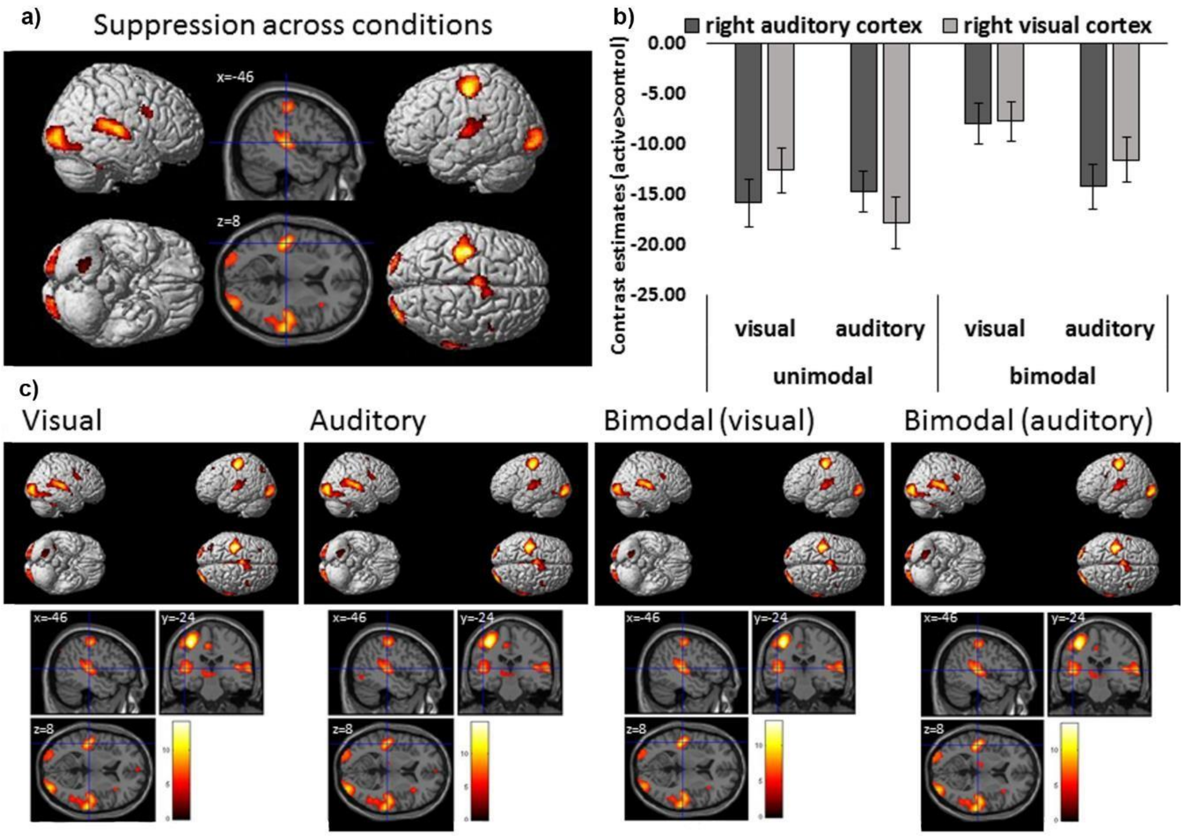


Figure 6. Results of the fMRI analysis regarding BOLD suppression a) Conjunction analysis for the suppression effect across conditions ([(Pas$_{Uni}$Vis > Vol$_{Uni}$Vis) ∩ (Pas$_{Uni}$Aud > Vol$_{Uni}$Aud) ∩ (Pas$_{Uni}$AV > Vol$_{Bi}$Vis) ∩ (Pas$_{Uni}$AV > Vol$_{Bi}$Aud)]); b) Contrast estimates of activation clusters for suppression effects in the right auditory (dark gray) and visual (light gray) cortex, respectively. c) Suppression effects for each individual condition. All contrasts at $p_{FWE} < .05$. Error bars represent standard error of the mean. Vol$_{Uni}$Vis = voluntary unimodal visual, Vol$_{Uni}$Aud= voluntary unimodal auditory, Vol$_{Bi}$Vis = voluntary bimodal visual, Vol$_{Bi}$Aud = voluntary bimodal auditory, Pas$_{Uni}$Vis = passive visual, Pas$_{Uni}$Aud = passive auditory, Pas$_{Uni}$AV = passive audiovisual.

Although BOLD suppression effects were found to be weaker in bilateral visual (MNI: x, y, z = 38 -54 -14, T = 5.21, $p_{FWE} < 0.05$; MNI: x, y, z = 46 -52 -12, T = 4.32, $p_{FWE} = 0.258$) and auditory cortices (MNI: x, y, z = 52 -50 18, T = 4.69, $p_{FWE} = 0.080$; MNI: x, y, z = -64 -44 10, T = 2.70, p < 0.01 uncorrected) when button presses were not modelled, it was still present. However, activity in the left motor cortex was not present anymore, and instead switched to the right hemisphere (MNI: x, y, z = 36 -16 52, T = 5.46, $k_E = 860$). These results suggest that activity differences in the voluntary and passive conditions should be interpreted with caution.

In the second analysis, BOLD suppression for undetected compared with detected trials (detected > undetected) were tested using an inclusive mask of visual and auditory cortices found to weaker in the conjunction analysis. Reduced BOLD activity was found for undetected compared with detected trials in bilateral occipital (MNI: x, y, z=-16 -96 -6, T = 4.76, k_E = 311, p < 0.001 uncorrected; MNI: x, y, z = 24 -92 -14, T = 4.31, k_E = 99, p < 0.001 uncorrected) and temporal (MNI: x, y, z = 60 -28 8, T = 4.37, k_E = 81, p < 0.001 uncorrected; MNI: x, y, z = -56 -32 12, T = 3.88, k_E = 60, p < 0.001 uncorrected) areas of the brain (see Table II and Figure 7) When button presses were not modelled, the results were slightly different; bilateral occipital (MNI: x, y, z = -16 -94 -6, T = 4.22, p < 0.001 uncorrected; MNI: x, y, z = 26 -92 -12, T = 3.59) and temporal (MNI: x, y, z = 60 -28 8, T = 3.65; MNI: x, y, z =-52 -32 14, T = 3.08) for detected > undetected contrast.

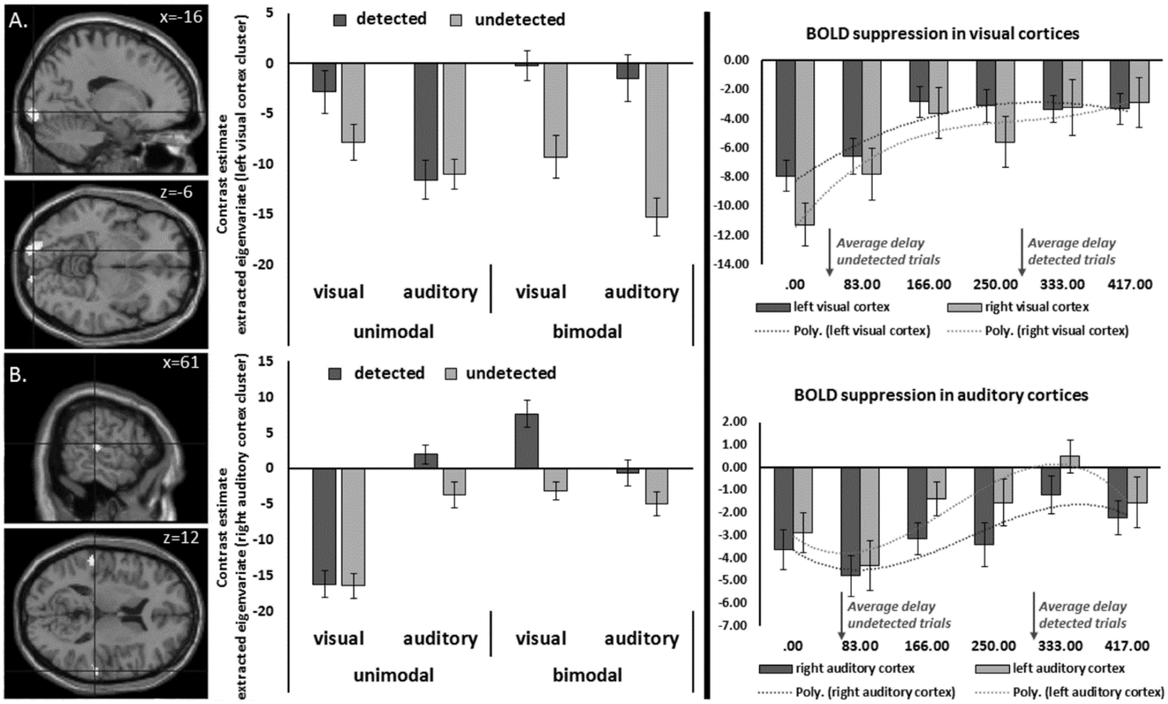


Figure 7. Suppression effects for subjectively undetected compared with detected trials in a) visual and b) auditory cortices. Data are inclusively masked by the suppression effect illustrated in Figure 6a. Bar graphs at the right illustrate suppression effects in visual (top) and auditory (bottom) cortices across conditions as a function of the delay between the action and the stimulus. Error bars represent the standard error of the mean. For all contrasts, p < 0.001 uncorrected with minimum cluster extension of 50 voxels.

Delay detection-related BOLD activity (detected > undetected contrast) at the whole brain level revealed activity differences in left parahippocampus (MNI: x, y, z = -30 -34 -12, T = 5.58, $k_E = 27$, $p_{FWE} < .05$), the right precuneus (MNI: x, y, z = 14 -60 22, T = 5.53, $k_E = 19$, $p_{FWE} < .05$) and the left putamen/insula (MNI: x, y, z = -28 -2 -2, T = 5.16, $k_E = 7$, $p_{FWE} < .05$). At a more liberal threshold (p < 0.001, 50 voxels), medial prefrontal lobe, anterior and posterior cingulate cortex (ACC/PCC), temporal poles, parietal and hippocampal structures emerged (see Figure 8).

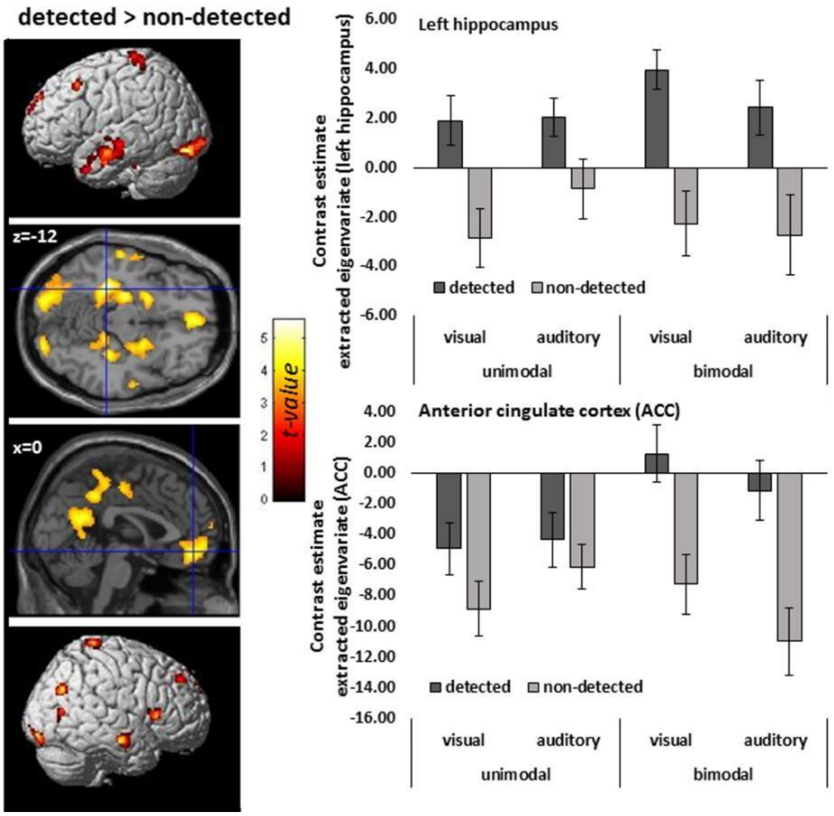


Figure 8. FMRI results for subjectively undetected compared with detected trials (p < 0.001 uncorrected with minimum cluster extension of 50 voxels). Bar graph illustrates contrast estimates of the left hippocampus at a cluster level ($p_{FWE} < 0.05$) and the bilateral ACC cluster (p < 0.001 uncorrected; for statistics see Table II).

Undetected > detected contrast revealed activity differences in the right inferior frontal gyrus (MNI: x, y, z = 52 20 6, T = 4.42, k_E = 149, $p < 0.001$ uncorrected; MNI: x, y, z = 34 26 -6; T = 3.93, k_E = 73, $p < 0.001$ uncorrected).

Analysis exploring the interaction between task and modality on subjective delay detection revealed no effects on the conservative FWE level. At a more liberal threshold ($p < 0.001$ uncorrected, 50 voxels), a significant interaction between detection and modality was found in the left cerebellum (62.0% in left lobule VI, 9.3% in lobule V) extending to the fusiform gyrus (MNI: x, y, z = -32 -48 -26, F = 20.41, k_E = 182, $p < 0.053$ FWE cluster corrected; see Figure 9). Contrast estimates corresponding to the respective cluster showed significant differences between detected vs. undetected trials for the bimodal (detected > undetected, MNI: x, y, z = -30 -34 -28, T = 5.82, k_E = 156, $p_{FWE} < .001$), compared with the unimodal condition.

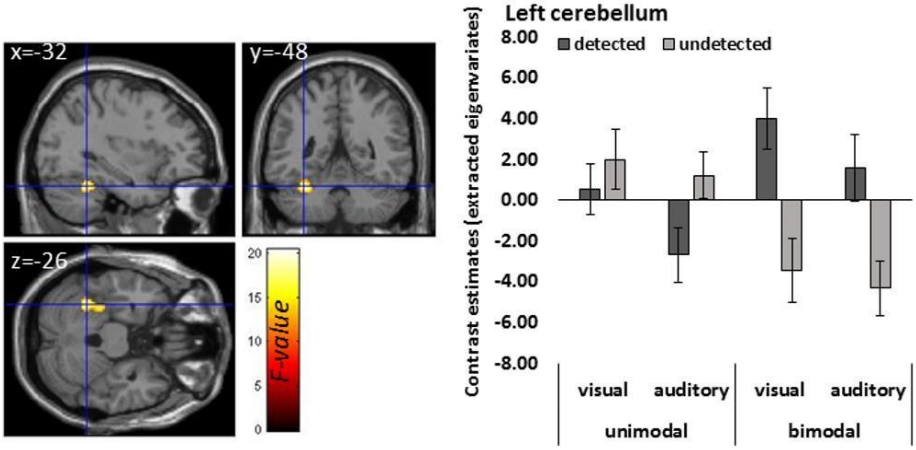


Figure 9. fMRI results showing activation of the left cerebellum with cluster extensions in the left fusiform gyrus for the interaction of delay detection and modality. Bar graph depicts contrast estimates of the respective cluster illustrate a specific activation for detected compared with undetected trials in the bimodal conditions. Error bars represent the standard error of the mean. $p < 0.001$ uncorrected with minimum cluster extension of 50 voxels.

4.5 Discussion

Study 2 assessed neural correlates of perceiving unimodal vs. bimodal action outcomes triggered by voluntary movements vs. viewed passively, and subjective delay detection-related BOLD responses. Accordingly, voluntary button presses performed by participants led to either unimodal visual/auditory or bimodal AV stimuli after various delays, and the task of the participants was to detect delays between the button press and the sensory outcome of a specific modality. In passive trials, participants were asked to report the number of modalities, which could be only visual, only auditory or AV, presented after a cue. Proportion of delay detection was found to be higher for bimodal compared with unimodal trials, and when the task was visual compared with when it was auditory. Analysis on fMRI data revealed BOLD suppression in somatosensory, visual and auditory processing regions when the stimuli were triggered by voluntary movements as opposed to when the stimuli were passively perceived. Moreover, BOLD suppression was found to be higher for subjectively detected compared with undetected trials. Analysis of BOLD activity associated with subjective delay detection revealed an interaction between detection and modality in the left cerebellum, suggesting that when the outcome was unimodal, activity in this area was less pronounced for detected trials than when it was bimodal, in which case, an opposite pattern emerged. This result, along with higher delay detection responses for bimodal trials point to the influence of additional modality on the perception of voluntary actions and their outcomes.

As expected, BOLD suppression was found in visual, somatosensory and auditory regions of the brain during voluntary actions. Suppression effects were also similar across modalities compared with similar sensory inputs observed passively. This result points to predictive processing of voluntary action outcomes whereby equally likely action outcomes were anticipated and subsequently suppressed (Bays et al., 2006; Voss et al., 2008). Moreover, reduced BOLD responses in auditory and visual cortices were strongest for subjectively undetected trials. This was to be expected, as subjective detection of delays increased linearly with the inclusion of physical delays.

Existing research on multisensory processing has demonstrated that a certain stimulus modality can facilitate the processing of another modality, especially when they are temporally and/or spatially in synchrony (Diederich and Colonius, 2004; Meredith et al., 1987; Stein, 2012). Results of Study 2 were in line with this, in that additional sensory modality facilitated behavioral performance, as evidenced by increased detection responses when the action outcome was audiovisual.

Regarding detection-related BOLD activity, cerebellum was found to be involved in subjective detection of delays, and more so when the sensory outcome was bimodal. This result supports previous findings on cerebellum's role in error-related processing of voluntary action outcomes (Blakemore et al., 2001; S. Blakemore et al., 1998; Wolpert et al., 1995). In addition, it suggests that the additional sensory modality was associated with increased error-related processing. Therefore, it seems in general that multisensory stimuli facilitated detection performance, which was accompanied by increased activity in the cerebellum. Other areas found to be involved for subjectively delayed trials were the ACC and the hippocampus. ACC has been consistently implicated in monitoring of action and behavior (Botvinick et al., 2001; Carter et al., 1998; Holroyd and Coles, 2002; Matsumoto et al., 2007). Higher involvement of this area for subjectively detected trials support the role of ACC in detecting temporal discrepancies between actions and their sensory outcomes.

Together, findings of Study 2 provide supporting evidence for BOLD suppression with regard to voluntary action outcomes, and error-related action outcome processing in the cerebellum. Importantly, the present findings extend BOLD suppression to multisensory action outcomes, suggest predictive processing of equally likely sensory outcomes linked with voluntary movements, and show modulatory effect of the additional sensory modality on error-related processing in the cerebellum.

Despite these novel findings, one limitation that needs consideration is the different task demands across voluntary and passive conditions. Whereas in the voluntary condition participants were asked to focus on a single modality and detect delays between the button press and this single modality, in the passive condition they were required to report the number of modalities presented in a trial. In this sense, the tasks required different aspects of the sensory stimuli to be attended. Moreover, stimulus presentation in the passive condition was unpredictable in time, compared with stimulus presentation in the voluntary condition which was more or less predictable by the button press. Research on action outcome processing underlies the influence of temporal predictability, predictability of the stimulus occurrence in time, which is different than prediction regarding action outcome related processing (Hughes et al., 2012). Future studies should distinguish temporal predictability of the sensory stimuli from predictive processing of action outcomes. A related limitation of Study 2 was the fact that when button presses were not modelled as a condition of no interest, results regarding BOLD suppression effects were weaker. Efference copy-related predictive processing can be better investigated with contrasting voluntary movements with their externally-generated counterparts. This enables re-afferent feedback to be similar across different movements, and makes it possible to study the contribution of the efferent signal (Weiskrantz et al., 1971).

To conclude, Study 2 investigated neural correlates of perceiving unimodal vs. bimodal outcomes associated with voluntary button presses as opposed to passive viewing of these sensory inputs. Findings showed BOLD suppression in sensory cortices which was independent of task and modality, along with increased BOLD activity in these areas for subjectively delayed as opposed to undelayed trials. In addition, detection of delays were coupled with increased activity in the ACC and hippocampus, which is in line with existing evidence on the role of these areas in action monitoring. Furthermore, the cerebellum was found to be modulated not only by voluntary actions, but also by whether the outcome was unimodal or bimodal, with increased activity in bimodal trials, corroborating its role in processing temporal discrepancies in the predicted action outcome relationship. Together, these findings support predictive processing of voluntary action outcomes and extend it to multisensory outcomes of voluntary movements.

5 STUDY 3: NEURAL CORRELATES OF MULTISENSORY ACTION OUTCOMES: ADDRESSING EFFERENCE COPY-RELATED PREDICTIONS AND NATURALISTIC ACTION OUTCOMES

The content of Study 3 has been submitted for a publication as:

Arikan, B.E., van Kemenade, B.M., Podranski, K., Steinsträter O., Straube, B., Kircher, T. (under review). Neural correlates of perceiving multisensory action outcomes in an ecologically valid set-up: BOLD suppression in sensory cortices and multisensory influences.

5.1 Background

In Study 2, neural correlates of perceiving unimodal vs. multimodal action outcomes was investigated in which unimodal and bimodal visual and auditory stimuli presented at various delays after a button press were compared to identical, but action unrelated, unpredictable control stimuli (Straube et al., 2017). Reduced BOLD activity was found in somatosensory, visual and auditory cortices for voluntary action outcomes compared with passive viewing of similar sensory stimuli, suggesting sensory suppression at a neural level. In addition, increased BOLD responses were found in sensory areas associated with additional task unrelated modality, independent of whether the outcome actually occurred or not. The conclusion was that the internal model and related cerebellar functions might take all possible action outcomes into account when these outcomes are equally likely. On a behavioral level, increased delay detection responses were observed for bimodal trials when the stimuli were self-generated, suggesting that the additional modality is advantageous for the monitoring of action outcomes. Moreover, a modulation in the left cerebellum by judgments of delay and modality, along with an increased cerebellar activity in bimodal compared with unimodal trials for voluntary movements point to differential involvement of cerebellum for processing multisensory action outcomes.

Despite these novel findings on multisensory processing of action outcomes, Study 2 had a number of limitations. First, the control condition in Study 2 involved passive viewing of sensory stimuli. Although this condition might address the influence of voluntary movements on the perception of sensory inputs by factoring out mere sensory processing, it cannot refer to the specific influence of efference copy-related predictive processes. Externally-generated movements, on the other hand, might prove more efficient in distinguishing efference copy-related predictive processes that are specific to voluntary movements. Sensory stimuli that are self-generated produce both efferent and re-afferent information whereas sensory outcomes generated externally provide only re-afferent information (Weiskrantz et al., 1971). By contrasting both movement types, the influence of efference copy-related predictive processes can be more effectively identified. Second, actions and their consequences in the real world are more complex than a button press triggering a dot. Although button presses as well as computer-generated sensory inputs are easier to control and manipulate, more studies are needed to demonstrate that similar mechanisms are at work in real life, and for relatively complex movements (Benazet et al., 2016; Ingram and Wolpert, 2011).

The main purpose of Study 3 was to investigate neural correlates of perceiving voluntary and externally-generated movements of the hand leading to unimodal or bimodal outcomes, and at the same time address issues raised with regard to Study 2. To this end, participants were asked to perform wrist movements using the handle of a custom-made passive movement device (PMD). Half of the trials involved an externally-generated movement condition in which the PMD moved the hand automatically. This condition allowed for addressing the specific role of efference copy-related processing during voluntary movements, as opposed to re-afferent feedback arising as a result of both movements. The movements were recorded with a camera and displayed to the participants in real-time, which allowed for a better representation of realistic action outcome associations and for testing whether similar processes are at work in an ecologically-valid experimental set-up compared with relatively abstract movement outcome associations previously used. Action outcome discrepancies were induced by systematically introducing delays between the movement and the visual feedback of the movement (unimodal condition). The task of the participants was to report whether they detected a delay between the actual movement and the visual feedback or not. Half of the trials involved an auditory beep coupled to the onset of the visual feedback (bimodal condition). With this condition, the aim was to assess whether an additional modality, even though not directly related to the task, would influence perception of temporal discrepancies between the action and the visual feedback as it bares information about delays. Based on findings of Study 2 concerning BOLD suppression (Straube et al., 2017), it was expected that there would be reduced processing in sensory areas for voluntary compared with externally-generated movements. In addition, whether voluntary movements were expected to yield increased BOLD activity in areas such as DLPFC, ACC and SMA previously attributed to voluntary movements (Cunnington et al., 2005, 2002; Deiber et al., 1999; Jenkins et al., 2000a; Lau et al., 2004; Lau et al., 2004; Mueller et al., 2007; Weiller et al., 1996). Because unimodal and bimodal outcomes would be equally likely, reduced BOLD activity would be expected in auditory processing areas both for unimodal and bimodal conditions. It was also hypothesized that the auditory stimulus triggered by the voluntary movement would provide additional timing information about the temporal discrepancy between the movement and visual feedback, aiding in delay detection performance. Finally, neural correlates of subjective delay detection across different movements and modalities would be investigated in order to assess whether detection-related BOLD responses were be influenced by movement and modality.

5.2 Materials and Methods

5.2.1 Participants

23 right-handed students (11 females, mean age = 25.83±3.09 years) from Philipps University Marburg participated in the behavioral training and fMRI scanning. One participant who took part in the behavioral training was not included in the fMRI study due to an increased bias to report delays even for the 0ms delay (see Experimental Design and Procedure for details). Informed consent was obtained from all participants. Participants reported normal or corrected-to-normal vision and normal hearing, as well as no history of psychiatric or neurological disorders, and no current use of psychoactive medications. Right-handedness was confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971). The experiment was approved by the local ethics committee and performed in accordance with the Declaration of Helsinki. The participants were paid for their participation. Three

participants were excluded from the final analyses due to excessive head movement (n = 1) or technical issues (n = 2), resulting in a final sample of 20 participants (9 females, age=26±3.24).

5.2.2 Apparatus

A custom-made MR-compatible PMD was used for the execution of both voluntary and externally-generated movements. The device was built using non-ferromagnetic materials (PVC, titan). A handle was designed for the execution of the movement, with a horizontal trajectory. Importantly, the movement range of the handle, and therefore the to-be-executed movement, was restricted, so that movement range would remain constant throughout trials and for different movement types. Approximate movement range was ~30° and ~5.5 cm (see Figure 10a). Motion to the device could be induced automatically with compressed air (6 bar). Approximate force used when the device was working automatically was 20N.

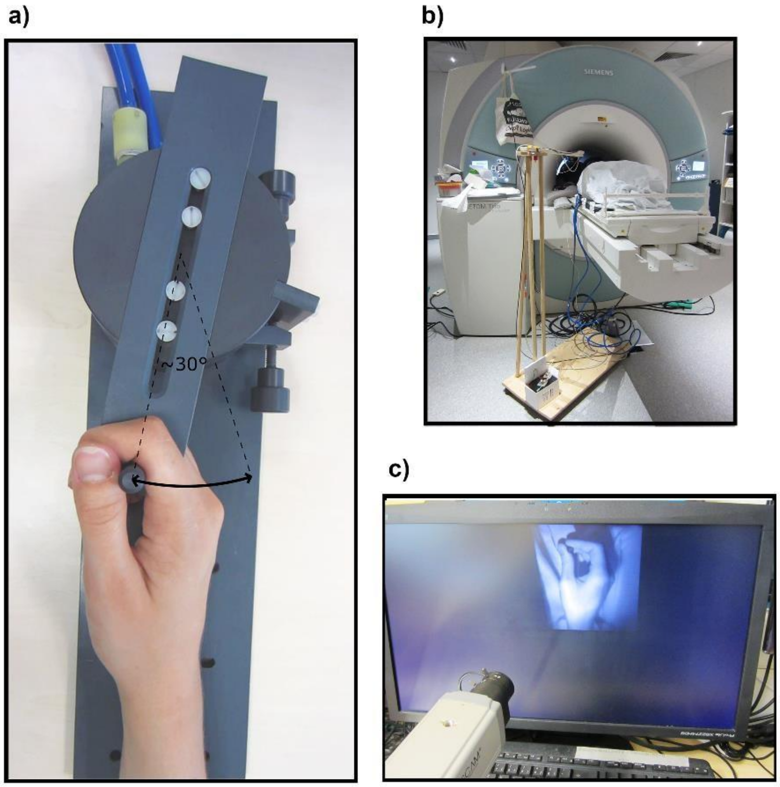


Figure 10. a) Custom-made PMD. Movement trajectory was horizontal, and the range of movement from one end to another was ~30. b) Outlook of the experimental set-up. MRI-compatible camera recorded and displayed hand movements in real time during self- or externally-generated movements. c) Visual display shown to the participant, comprising the visual outcome of the movement.

An MR–compatible camera (MRC High Speed, MRC Systems GmbH, Heidelberg, Germany) with 2ms refresh rate was used to record movements of the hand. The camera was mounted to an adjustable custom-made support. Auditory beeps were presented via MR-compatible headphones (MR-Confon, Optimel, Magdeburg, Germany). Responses were given using MR-compatible button pads (Cedrus, Lumina, San Pedro, USA). Visual display of the movement recorded by the camera in real-time was presented on a mirror-projected computer screen (60Hz refresh rate). Five LEDs were attached to the device, for the purpose of detecting movement onsets. A motion detection algorithm written specifically for this study was applied to the camera images, detecting the spatial position of one moving LED with regard to the four fixed LEDs in each camera frame. For each trial, movement onset was defined as a minimum of 1° change in the relative position of the moving LED within one frame (requiring an increase of at least 0.5° per frame). Delays were presented from movement onset onwards. All equipment was controlled by custom written software running on a personal computer (Dell Optiplex 9020, Intel Core i5-4570, 4 Cores, 3.2 GHz, 4GB RAM).

5.2.3 Experimental Design and Procedure

An event-related design was used. On each trial, the participant was asked to perform wrist movements (extension and flexion) with the right hand using the handle of the PMD. The movements were recorded by the camera, and presented to the participant in real time via mirror-projection, constituting the visual outcome of the movement (see Figure 10b & c). Six delays (0, 83, 167, 250, 330 and 417ms, determined based on the screen refresh rate) were introduced between the movement and the real time display of the movement. The participants were asked to judge whether there was a delay between actual movement of their hand movement and visual outcome of the movement. Half of the trials contained 440Hz sine-wave pure tones (500ms), which were presented with the same delay used to delay the visual outcome. The task remained the same in these trials.

One week prior to scanning, participants completed a behavioral training in order to familiarize themselves with the task. To this end, the participants were initially trained to perform hand movements both in the voluntary and externally-generated conditions. Accordingly, they were instructed to grab the handle of the PMD, and move the handle from left to right and then back in approximately 1500ms, while trying to maintain a constant pace with the help of a metronome. They then practiced externally-generated movement condition by grabbing the handle of the PMD while trying to relax the hand and wrist as much as possible, and letting the device move their wrist. In order to prevent participants from using visual cues from the hand, a curtain was placed to hide the right hand from participants' sight. Participants executed both movements first without and then with the visual display recorded by the camera and presented in real-time via a computer screen. The participants were instructed to observe the displayed movement on the screen, and to judge whether there was a delay between their actual movement and the visual outcome of the movement or not. They were also told that in some trials they would also receive auditory beeps, but this was not related to the task. Participants first completed trials with no delay and 417ms delay, and received feedback indicating whether they answered correctly. They then completed three runs that were similar in length to the main experimental runs in the scanning sessions. Each run contained a voluntary and an external movement block (mini-blocks) in alternating order (144 trials in total). The order of movement type was counterbalanced across participants. Because being able to detect the delays was crucial for the paradigm, only participants who detected at least 50% of delays or more at the most extreme delay, and who reported detecting a delay less than 50% of the 0ms delay trials, were invited to the fMRI experiment. One participant did not fulfill this criteria, and was therefore not invited to the fMRI experiment. The training procedure took approximately one hour.

In the fMRI experiment, participants were positioned inside the bore in supine position, with their right hand placed on the PMD handle which was located besides them. Each participant received five experimental blocks, each of which contained two mini-blocks (voluntary and externally-generated movements, each having 24 trials) in counterbalanced order. At the beginning of each mini-block, the participant was informed about the movement type they had to perform (voluntary or externally-generated). Each trial started with a cue, ‘Ready’, that lasted for 1500ms. This cue indicated that participants had to prepare themselves for the upcoming movement. Immediately after the disappearance of the cue, the camera was turned on for 4000ms. This timing frame was chosen to give participants *some freedom* in performing a self-generated, intentional movement. The participant was instructed to perform the movement (in the voluntary mini-block), or let the device move their hand (in the external mini-block). The onset of the externally-generated trial was jittered (500-1000-1500ms). The participants saw their hand movement on the screen in real time or with one of five delays. After a 500ms interval, the question ‘Delay?’ appeared on the screen. Participants used their left index and middle finger to respond ‘Yes’ or ‘No’. Button assignment was counterbalanced across participants. Maximum time allowed for the response was 2000ms. Following the response, an intertrial interval of 2000-5000ms was presented. Unimodal and bimodal trials were randomized within blocks. Total number of trials for each participant was 240. Participants were allowed to have short breaks between the blocks. Each movement was monitored online and recorded, for the purpose of ensuring compliance with instructions, and for post-hoc screening of movement parameters. The scanning procedure took approximately one hour. The procedure is shown in Figure 11.

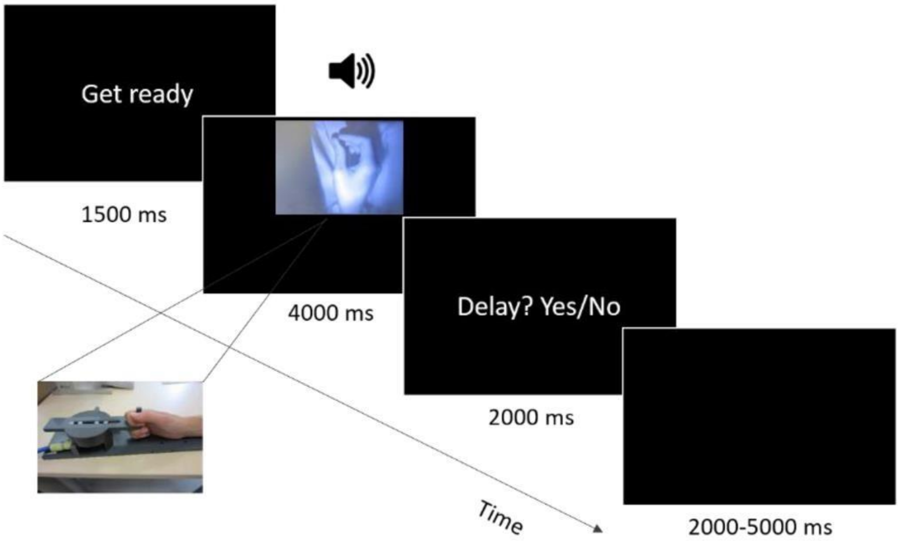


Figure 11. Timeline of an experimental trial. After the 'Get ready' cue, the camera was turned on for 4000ms, during which the participant had to perform either a voluntary or an externally-generated movement. They were asked to watch a video display of their movements on a mirror-screen, and judge whether there was a delay between the actual movement and the visual feedback of the movement. Auditory beeps coupled to the onset of the visual outcome, were presented during bimodal trials.

5.3 Analysis

5.3.1 Behavioral Data Analysis

Statistical analyses were performed using SPSS21 (IBM Corp. Released 2012). Behavioral data were grouped based on participant's responses regarding delay judgments, referred to as the subjective detection of delays. First, the proportion of 'delay' responses was calculated for each condition by dividing the number of trials in which the participant detected a delay between the movement and the visual feedback by the total number of trials.

5.3.2 fMRI Data Acquisition and Analysis

Functional imaging was carried out in a 3 T TIM Trio scanner (Siemens, Erlangen, Germany), using a 12-channel head-coil. A gradient echo EPI sequence was used (TR: 1650ms, TE: 25ms, flip angle: 70°). The whole brain was covered in 34 axial slices (gap: 15%, slice thickness: 4mm), each of which was acquired as a 64 x 64 matrix (FoV: 1152 x 1152mm^2, voxel size: 3 x 3 x 4.6mm) in descending order. 330 volumes were obtained during each experimental block. Anatomical images were obtained using a T1-weighted MPRAGE sequence (TR: 1900ms, TE: 2.26ms, flip angle: 9°, FoV: 256 x 256, slice thickness: 1mm, matrix: 256 x 256, voxel size: 1 x 1 x 1.5mm).

In order to account for possible stimulus-correlated movement artifacts in the voluntary movement condition, independent components analysis (ICA) on the raw data was performed using the MELODIC tool (Beckmann and Smith, 2004) in FSL (Jenkinson et al., 2012; Smith et al., 2004). The data were prepared for the ICA with the implementation of slice time correction, realignment using the MCFLIRT procedure, and spatial smoothing with an 8mm full-width-at-half-maximum (FWHM) isotropic Gaussian kernel. After ICA, components related to motion artifacts were removed. The remaining preprocessing steps and analyses were performed using statistical parametric mapping (SPM12, Wellcome Department of Imaging Neuroscience, University College London, UK) implemented in MATLAB 2012b (The Mathworks Inc., 2012). Accordingly, each participant’s anatomical image was co-registered to their first functional images, segmented and normalized to the standard Montreal Neurological Institute (MNI) standard space, and resampled to 2 x 2 x 2 mm^3 voxels.

Prior to statistical analyses, recorded video images from all participants were screened to examine whether the movements were properly and/or actually performed. Trials in which the participant did not move, and bimodal trials in which the movement detection algorithm did not work were excluded (1.4% of all trials).

Two statistical analyses were performed: The main purpose of the first analysis was to identify brain areas modulated by movement and modality. Initially, common activations during the execution of both movements were assessed. Then, the presence of BOLD suppression for voluntary action outcomes and whether BOLD suppression was similar across different modalities were examined by contrasting externally-generated with the voluntary movement condition. Possible differences in BOLD responses for voluntary movements that would yield differential activations in areas related to movement planning and execution were also examined. The second analysis was based on subjective delay detection, for the purpose of assessing areas differentially recruited during the perception of temporal discrepancies, and the influence of movement and modality on subjective detection of delays.

Both analyses were performed using the general linear model (GLM). For each participant, a boxcar function was defined for each experimental condition, time-locked to the onset of the corresponding epoch, and convolved with a canonical hemodynamic response function (HRF). Time series of all voxels were high-pass filtered with a cut-off frequency of 128 seconds. Regressors of interest modelling the time during the camera was on were defined with regard to movement (voluntary/externally-generated) and modality (unimodal/bimodal). Cue and response periods were defined as block regressors. In addition, six realignment parameters were defined as nuisance regressors to account for residual motion artifacts. Individual t-maps were generated for each condition of interest contrasted against an implicit baseline, and passed to a second level analysis, resulting in four regressors of interest: voluntary unimodal ($\mathrm{Vol}_{\mathrm{Uni}}$), voluntary bimodal ($\mathrm{Vol}_{\mathrm{Bi}}$), externally-generated unimodal ($\mathrm{Ext}_{\mathrm{Uni}}$), externally-generated bimodal ($\mathrm{Ext}_{\mathrm{Bi}}$). Contrast estimates corresponding to the four conditions were then entered into a full factorial design. As a proof of principle, a conjunction of voluntary and externally-generated movements was calculated to identify areas commonly activated in both types of movement ($(\mathrm{Vol}_{\mathrm{Uni}} + \mathrm{Vol}_{\mathrm{Bi}}) \cap (\mathrm{Ext}_{\mathrm{Uni}} + \mathrm{Ext}_{\mathrm{Bi}})$), and across unimodal and bimodal conditions ($\mathrm{Vol}_{\mathrm{Uni}} \cap \mathrm{Vol}_{\mathrm{Bi}} \cap \mathrm{Ext}_{\mathrm{Uni}} \cap \mathrm{Ext}_{\mathrm{Bi}}$). BOLD suppression effects were assessed by conducting a t-test for externally-generated vs. voluntary movement conditions using the contrast $[(\mathrm{Ext}_{\mathrm{Uni}} + \mathrm{Ext}_{\mathrm{Bi}}) - (\mathrm{Vol}_{\mathrm{Uni}} + \mathrm{Vol}_{\mathrm{Bi}})]$. Moreover, common areas showing reduced BOLD responses for voluntary movements across unimodal and bimodal outcomes were assessed with a conjunction analysis ($(\mathrm{Ext}_{\mathrm{Uni}} - \mathrm{Vol}_{\mathrm{Uni}}) \cap (\mathrm{Ext}_{\mathrm{Bi}} - \mathrm{Vol}_{\mathrm{Bi}})$). The presence of auditory-related activity in the voluntary vs. externally-generated conditions were investigated in order to address predictive processing for auditory outcomes in the voluntary compared with the externally-generated condition ($\mathrm{Vol}_{\mathrm{Uni}} - \mathrm{Ext}_{\mathrm{Uni}}$). Moreover, activity differences in the voluntary compared with externally-generated movements were examined using the contrast $[(\mathrm{Vol}_{\mathrm{Uni}} + \mathrm{Vol}_{\mathrm{Bi}}) - (\mathrm{Ext}_{\mathrm{Uni}} + \mathrm{Ext}_{\mathrm{Bi}})]$. Differences in BOLD activity for bimodal vs. unimodal outcomes were tested by $[(\mathrm{Vol}_{\mathrm{Bi}} +$

Ext_{Bi}) - (Vol_{Uni} + Ext_{Uni})] contrast. Because no specific hypothesis regarding the direction of the interaction between movement and modality, an F test was initially conducted to see whether there were any activations, which would presumably be followed by a t-test when necessary.

Subjective delay detection-related activity with regard to movement and modality was assessed by dividing those trials in which a delay was detected (detected) or not (undetected), and using the contrast detected > undetected (referred to as 'Det') for each factor at the first level. Detected and undetected trials were contrasted at the first level for the purpose of simplicity in interpreting the findings. Additional analysis in which delay detection was also modelled at the second level revealed similar results. Therefore, results of the simpler model are reported here. Data from two participants were excluded due to insufficient number of trials (e.g. no detected trials in the unimodal condition) with regard to subjective delay detection responses (sample for this analysis: 18 participants; 8 females, age = 26.22±3.34 years). On the second level, four regressors were modelled and entered into a full factorial design: $\text{DetVol}_{\text{Uni}}$, $\text{DetVol}_{\text{Bi}}$, $\text{DetExt}_{\text{Uni}}$, $\text{DetExt}_{\text{Bi}}$. Two t tests were conducted to assess whether detection-related activity for voluntary and externally-generated movement differed. These were [($\text{DetVol}_{\text{Uni}}$ + $\text{DetVol}_{\text{Bi}}$) – ($\text{DetExt}_{\text{Uni}}$ + $\text{DetExt}_{\text{Bi}}$)] for voluntary movements, and [($\text{DetExt}_{\text{Uni}}$ + $\text{DetExt}_{\text{Bi}}$) - ($\text{DetVol}_{\text{Uni}}$ + $\text{DetVol}_{\text{Bi}}$)] for externally-generated movements. Modality effects on detection-related BOLD activity were assessed with the contrasts [($\text{DetVol}_{\text{Uni}}$ + $\text{DetExt}_{\text{Uni}}$) – ($\text{DetVol}_{\text{Bi}}$ + $\text{DetExt}_{\text{Bi}}$)] for unimodal vs. bimodal, and [($\text{DetVol}_{\text{Bi}}$ + $\text{DetExt}_{\text{Bi}}$) - ($\text{DetVol}_{\text{Uni}}$ + $\text{DetExt}_{\text{Uni}}$)] for bimodal vs. unimodal. Possible action-related interactions between movement and modality on detection-related BOLD signal were also examined. The respective contrasts were [($\text{DetVol}_{\text{Uni}}$ - $\text{DetVol}_{\text{Bi}}$) – ($\text{DetExt}_{\text{Uni}}$ - $\text{DetExt}_{\text{Bi}}$)] and [($\text{DetVol}_{\text{Bi}}$ - $\text{DetVol}_{\text{Uni}}$) – ($\text{DetExt}_{\text{Bi}}$ - $\text{DetExt}_{\text{Uni}}$)].

To correct for multiple comparisons, family-wise error (FWE) correction at $p < 0.05$ implemented in SPM12 was used. In addition, to avoid type II errors, Monte Carlo simulations were run using the estimated smoothness of our functional data (14.6mm). This resulted in a minimum cluster size of 88 resampled voxels to achieve correction for multiple comparisons at $p < 0.05$, assuming an individual voxel type I error of $p = 0.001$ (Slotnick et al., 2003). The automated anatomical labelling (AAL) atlas (Tzourio-Mazoyer et al., 2002) and SPM Anatomy Toolbox (Eickhoff et al., 2005) were used to label significant activations, based on peak activation voxels. Visualization of significantly activated areas was performed by SPM12 and MRICron (Rorden and Brett, 2000).

5.4 Results

5.4.1 Behavioral

Figure 12a & b display proportion of delay responses as a function of movement and modality. A 2(Movement: Voluntary vs. Externally-generated) x 2(Modality: Unimodal vs. Bimodal) repeated measures ANOVA was conducted on the proportion of ‘delay’ responses. There was a main effect of movement; $F(1,19) = 6.83$, $p < 0.05$, $\eta^2 = .21$. Accordingly, subjective delay detection was significantly higher in the external ($M = .52$, $SEM= .03$) than in the voluntary ($M = .45$, $SEM = .04$) condition (Figure 12c). There was no main effect of modality, $F(1,19) = 2.24$, $p = .15$, nor was there an interaction; $F(1,19) =.08$, $p = .77$.

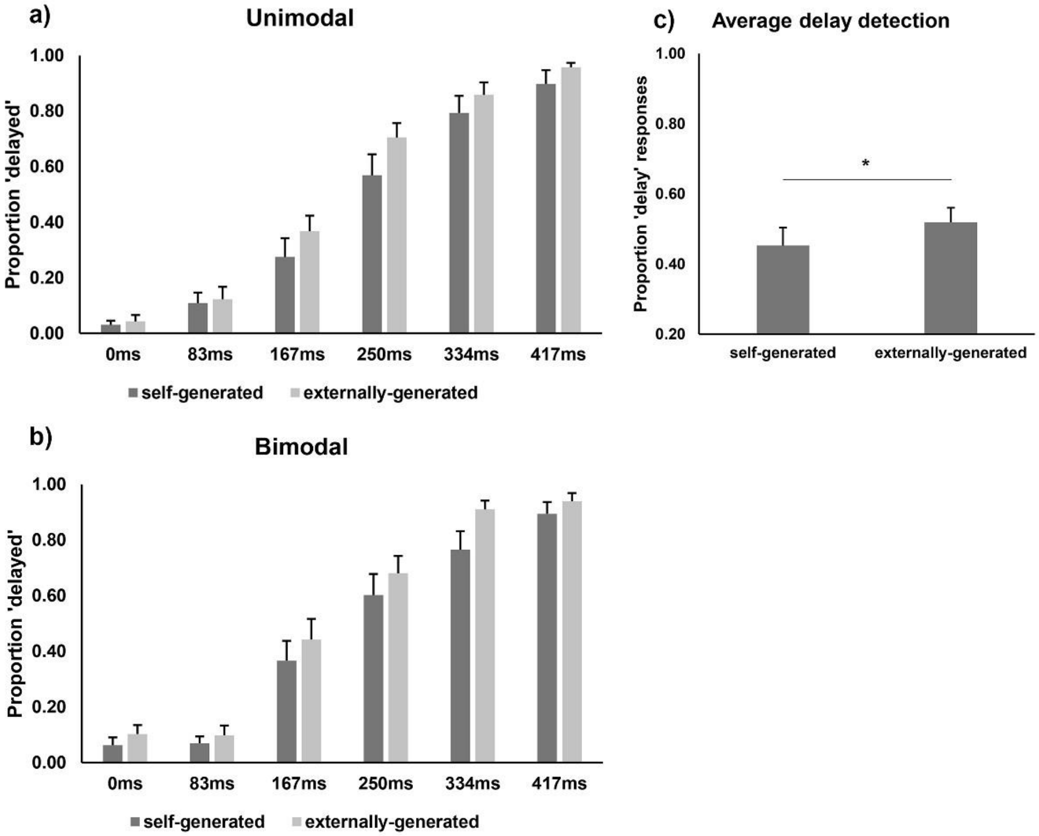


Figure 12. Graphs illustrating a) proportion of delay detection for each delay as a function of movement for unimodal, and b) for bimodal trials, and c) significant proportion of delay detection between voluntary and externally-generated movements. Error bars denote standard error of the mean.

In order to test whether movement duration was similar across voluntary and externally-generated movements, recorded trials were used to determine the approximate onset and offset of each movement (18 participants). A post-hoc paired-samples t-test showed that average movement durations across voluntary and externally-generated trials were not significantly different from each other; t(17) = 1.23, p = .23, *d* = .3; average movement duration for voluntary movements (M = 1373.82, SEM = 81.84), average movement duration for externally-generated movements (M = 1282.78, SEM = 44.22).

5.4.2 fMRI

First, common areas implicated during voluntary and externally-generated movements were explored using the conjunction ($[Vol_{Uni} + Vol_{Bi}] \cap [Ext_{Uni} + Ext_{Bi}]$). Common activations were found in sensory processing areas including the bilateral inferior and middle occipital gyri, postcentral gyri, along with inferior frontal and parietal areas, and bilateral thalamus and insula. The anatomical locations of these clusters are shown in Table I. Examination of common areas implicated across all conditions revealed similar areas (see Figure 13).

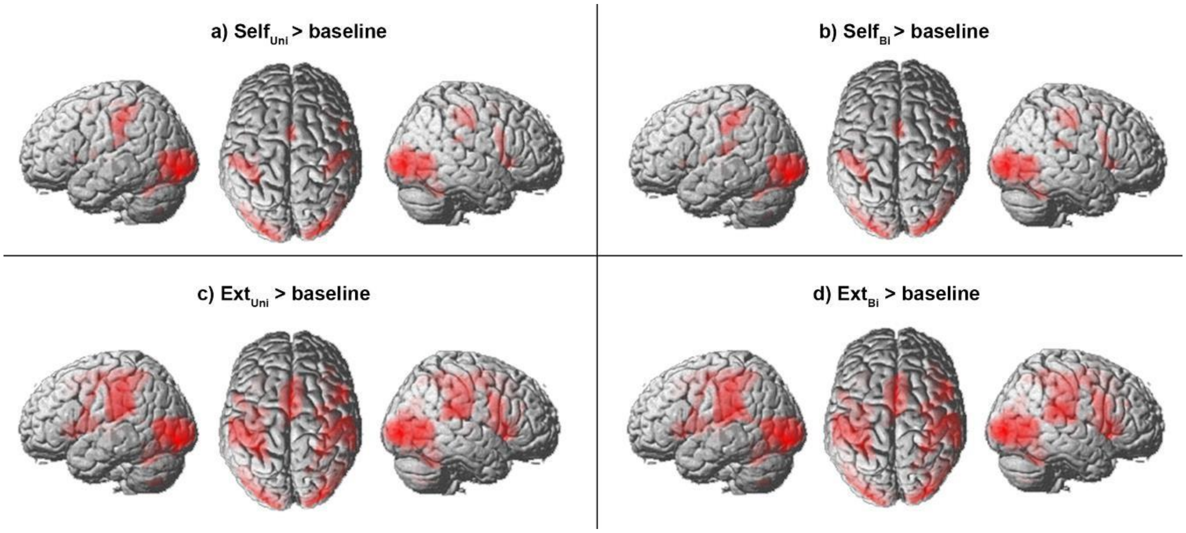
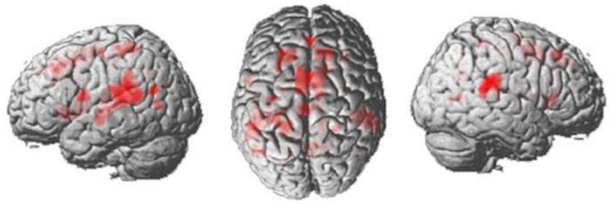
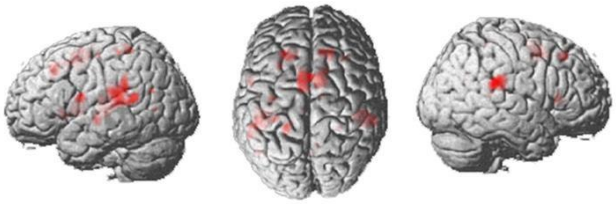


Figure 13. fMRI results showing a) voluntary unimodal, b) voluntary bimodal, c) externally-generated unimodal, and d) externally-generated bimodal trials against implicit baseline. All maps were thresholded at $p_{FWE} < 0.05$ (height threshold = 4.79).

BOLD suppression effects were addressed by contrasting externally-generated with voluntary movement trials, which revealed activations in sensory areas including the secondary somatosensory cortices, middle and superior temporal gyri (MTG and STG, respectively) extending to primary auditory cortices along with middle and superior occipital gyri including V5. In addition, activations were found in pre- and primary motor areas, inferior parietal lobules (IPL), precuneus and insula (see Figure 14a). The anatomical locations of these clusters are shown in Table III.



a) $(Ext_{Uni} + Ext_{Bi}) - (Self_{Uni} + Self_{Bi})$



b) $(Ext_{Uni} - Self_{Uni}) \cap (Ext_{Bi} - Self_{Bi})$

Figure 14. fMRI results showing a) BOLD suppression effect for voluntary compared with externally-generated movements, b) conjunction of unimodal and bimodal feedback for externally-generated vs. voluntary movements. All maps were thresholded at $p_{FWE} < 0.05$ (height threshold = 4.79).

Common BOLD suppression effects in sensory areas across unimodal and bimodal conditions were also identified, using the conjunction $((Ext_{Uni} - Vol_{Uni}) \cap (Ext_{Bi} - Vol_{Bi}))$. Significant BOLD suppression was observed in premotor areas including the SMA, bilateral primary and secondary somatosensory cortices, middle and inferior occipital gyri as well as the calcarine sulci, MTG, STG, and IPL (see Figure 14b). These results suggest efference copy-related predictive processing for voluntary movements, based on the finding that activity in auditory areas was reduced during both unimodal and bimodal conditions.

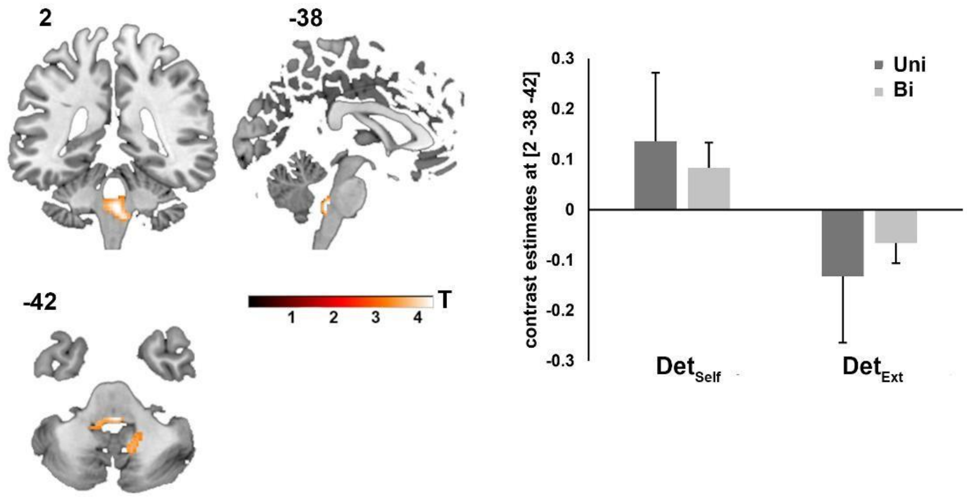


Figure 15. a) Significant activation cluster regarding detection-related BOLD responses for self- compared with externally-generated movements ([(Det$_{Vol}$Uni + Det$_{Vol}$Bi) – (Det$_{Ext}$Uni + Det$_{Ext}$Bi)]) in the cerebellar vermis ($p < 0.05$ cluster corrected) overlaid on a standardised T1-weighted image, with respective bar graphs depicting contrast estimates (±SEM) across conditions for the respective cluster.

The contrast assessing voluntary compared with externally-generated movements revealed no significant activations (at $p_{FWE} < .05$ or $p < .001$ uncorrected level), suggesting that neither motor or sensory processing areas, nor action monitoring-related regions were more recruited when the movement was self-generated.

The bimodal vs. unimodal ([Vol$_{Bi}$ + Ext$_{Bi}$] - [Vol$_{Uni}$ + Ext$_{Uni}$]) contrast revealed significant activations in bilateral temporal cortices, with two large clusters in bilateral STG (MNI: x, y, z = 62, -16, 8, T = 12.65, k_E = 2166, $p_{FWE} < 0.05$; MNI: x, y, z = -52, -20, 6, T = 11,32, k_E = 1688, $p_{FWE} < 0.05$), and a small cluster in left inferior frontal gyrus (MNI: x, y, z = -36, 14, 28, T = 4.9, k_E = 2, $p_{FWE} < 0.05$). No significant interactions were found for movement and modality.

Second analysis regarding detection-related activations yielded two main effects, and an interaction. The DetVol > DetExt contrast revealed an area in the pons/cerebellar vermis (MNI: x, y, z = 2 -38 -42, T = 4.46, k_E = 146, $p < 0.05$ cluster corrected) (see Figure 15). There was also a near threshold activation in the right cerebellum IX (MNI: x, y, z = 14 -56 -42, T = 3.94, k_E = 79, $p < 0.05$ cluster corrected). No significant areas were found for the reverse contrast (DetExt > DetVol). The Det$_{Uni}$ > Det$_{Bi}$ contrast yielded significant detection-related BOLD responses in the left cerebellum VIII (MNI: x, y, z = -24 -58 -40, T = 4.14, k_E = 108, $p < 0.05$ cluster corrected), the right temporal cortex (MNI: x, y, z = 50 -24 -12, T = 4.12, k_E = 174, $p < 0.05$ cluster corrected), and in middle occipital gyrus (MNI: x, y, z = 30 -84 8, T = 4.04, k_E = 138, $p < 0.05$ cluster corrected) (see Figure 16). The $\text{Det}_{\text{Bi}} > \text{Det}_{\text{Uni}}$ contrast revealed no significant activation differences. Finally, the interaction contrast $[(\text{DetVol}_{\text{Uni}} - \text{DetVol}_{\text{Bi}}) – (\text{DetExt}_{\text{Uni}} - \text{DetExt}_{\text{Bi}})]$ yielded activation differences in the left cerebellum VIII (MNI: x, y, z = -26 -52 -44, T = 4.38, k_E = 171, $p < 0.05$ cluster corrected), suggesting that detection-related activity for voluntary movements in this area was more pronounced for unimodal than for bimodal outcomes, which was similar during externally-generated movements (see Figure 17).

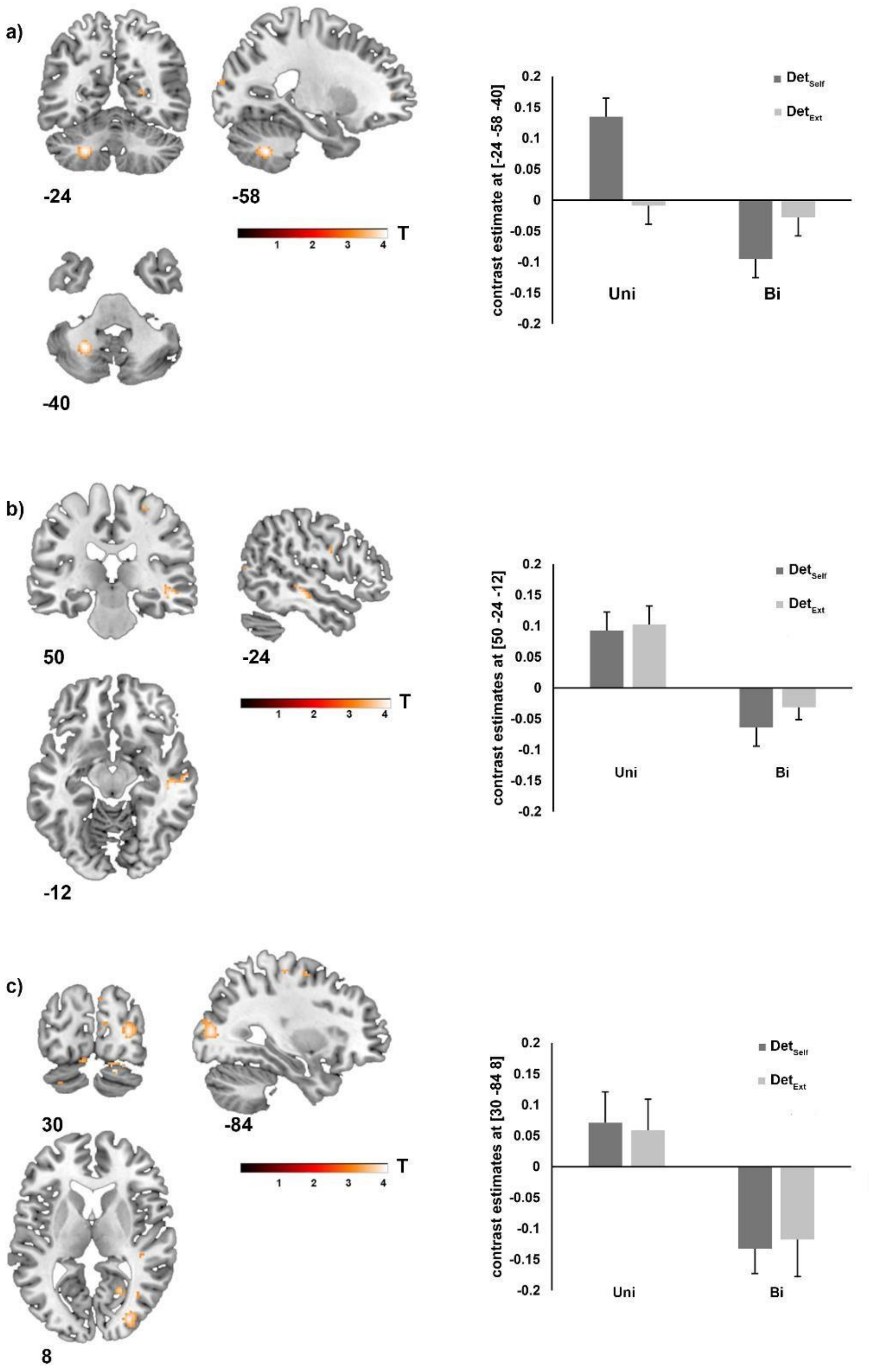


Figure 16. Significant activation clusters regarding detection-related BOLD responses for unimodal compared with bimodal trials ([(Det$_{\text{Vol}}$Uni + Det$_{\text{Vol}}$Bi) – (Det$_{\text{Ext}}$Uni + Det$_{\text{Ext}}$Bi)]) in a) left cerebellum VIII ($p < 0.05$ cluster corrected), b) right middle temporal gyrus, c) right middle occipital gyrus overlaid on a standardised T1-weighted image with bar graphs depicting contrast estimates (±SEM) across conditions for the respective cluster.

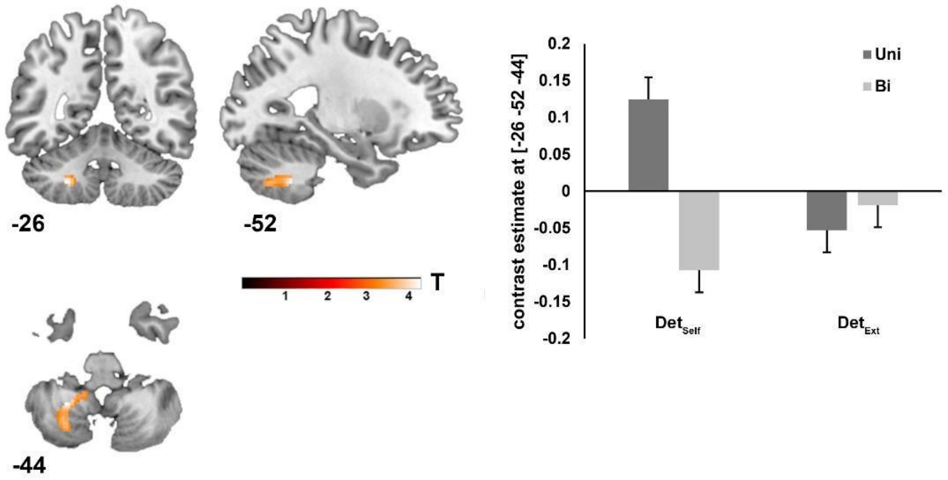


Figure 17. Activation cluster regarding detection-related interaction between movement type and modality ([(Det_{Vol}Uni - Det_{Vol}Bi) – (Det_{Ext}Uni - Det_{Ext}Bi)]) in the left cerebellum VIII ($p < 0.05$ cluster corrected) overlaid on a standardised T1-weighted image. Bar graphs illustrate contrast estimates (±SEM) for the interaction.

5.5 Discussion

In Study 3, neural correlates of perceiving unimodal vs. bimodal action outcomes during voluntary compared with externally-generated movements were assessed using realistic feedback of the hand as the visual outcome. Behaviorally, there was significantly higher proportion of delay responses for externally-generated compared with voluntary movements. fMRI findings revealed activations in several motor-related and sensory processing areas during both movements. As hypothesized, reduced BOLD responses were observed in somatosensory, auditory as well as visual processing areas for voluntary movements, suggesting sensory suppression on a neural level for voluntary action outcomes. This BOLD suppression effect was similar for unimodal and bimodal outcomes, indicating predictive mechanisms to be at work when the movement was voluntary. Results concerning detection-related BOLD responses showed significant activations during voluntary compared with externally-generated movements in the cerebellum, and for unimodal compared with bimodal trials in the right temporal and middle occipital areas along with the left cerebellum lobule VIII. Additionally, an interaction between movement and modality emerged in the left cerebellum lobule VIII, suggesting higher detection-related activity in this area for voluntary movements leading to unimodal outcomes. Together, these new findings extend previous findings regarding BOLD suppression for voluntary action outcomes to a well-controlled realistic context. Moreover, results of Study 3 support the relevance of the cerebellum in perceiving temporal discrepancies specifically for voluntary movements and their outcomes. The findings also point to multisensory influences on the neural processing of sensory inputs associated with voluntary movements.

Both voluntary and externally-generated movements led to activations in areas related to planning and control of motor tasks such as the SMA, IFG, and insula. These results are in line with the existing literature which suggest similar processing in premotor and motor structures for voluntary and externally-generated movements (Balslev et al., 2006; Ciccarelli et al., 2005; Gerardin et al., 2000; Szameitat et al., 2012; Weiller et al., 1996). In addition, common activations in somatosensory and auditory areas along with early and extrastriate visual cortices were found, indicating similar processing of sensory outcomes associated with both movements. When comparing externally-generated with voluntary movements, reduced activity was found during voluntary movements in sensory areas as expected. This BOLD suppression for self-generated stimuli is in line with findings of Study 2 (Straube et al., 2017) as well as with several other studies suggesting reduced activity for self-generated stimuli (Benazet et al., 2016; Blakemore et al., 1999; Blakemore et al., 2000; Shergill et al., 2013). These findings support the idea of efference copy-based predictive mechanisms, leading to suppression of action outcomes only when these are generated intentionally. In the same contrast, cingulate cortex, MTG, precuneus and the putamen were implicated as well. The MTG, precuneus and the putamen are involved in time perception (Matell and Meck, 2004; Stevens et al., 2007), and the processing of visuo-motor incongruencies (Balslev et al., 2006; David et al., 2007; Dreher and Grafman, 2002; Leube et al., 2003a; MacDonald and Paus, 2003). Externally-generated movements also led to increased BOLD activity in the IPL, an area found to be relevant for visuo-motor monitoring, processing of incongruencies between proprioceptive and visual signals during passive hand movements (Balslev et al., 2006; Farrer et al., 2008; Schnell et al., 2007), distinction between self and other-generated actions (Blakemore and Sirigu, 2003; Jackson, 2004; Leube et al., 2003b; Weiller et al., 1996), and mental imagery and complex actions (Blakemore and Sirigu, 2003; Haggard, 2009; Shergill et al., 2013; Sirigu et al., 1999).

Results of Study 3, therefore, provide support for the involvement of these areas in visuo-motor incongruencies, possibly contributing to self-other distinctions.

As described above, BOLD suppression was observed in sensory areas, in line with findings of Study 2 (Straube et al., 2017). Nonetheless, findings of these two studies differ especially with regard to visual processing of action outcomes. In the current study, reduced BOLD responses were found in V5, which has been linked with visual motion processing (Zeki et al., 1991), whereas in Study 2, BOLD suppression effects regarding visual action outcomes were present only in early visual areas (Straube et al., 2017). In the current study, voluntary and externally-generated movements led to extended activations in primary as well as extrastriate visual cortices, suggesting that visual feedback of the movement resulted in similar processing during both movements. It could be argued that the complexity of the visual input in the present study might be responsible for significant differences in the BOLD signal only for V5, while the relatively simpler dot in Study 2 led to suppressed BOLD responses in early visual areas. In addition, a direct comparison of the findings is rather difficult, as externally-generated movements instead of passive viewing of sensory stimuli were used. In the present study externally-generated movements were used as baseline to voluntary movements, whereby movement execution and re-afferent feedback were similar across conditions.

Study 3 additionally assessed whether reduced BOLD responses in auditory cortices was present for both outcomes. Results of the conjunction analysis suggest that reduced auditory cortex activity during voluntary movements was present in both unimodal and bimodal trials. This is similar to findings of Study 2 regarding suppressed BOLD activity in auditory cortices not only when there was audiovisual feedback, but also when the feedback was visual, and vice versa. In explaining this finding, it was proposed that the equal likelihood of unimodal and bimodal feedback for the voluntary movements might lead to the prediction and subsequent suppression of auditory processing areas in the brain (Straube et al., 2017). In the context of Study 3, it seems that there is supporting evidence for such predictive processing of auditory outcomes when the movement was voluntary. In other words, equal likelihood of unimodal and bimodal outcomes associated with a voluntary movement might have led to top-down expectation and subsequent processing for these outcomes (Blakemore et al., 1998; Blakemore et al., 2000; Blakemore et al., 1999; Wolpert, 2007; Wolpert and Flanagan, 2001). Research on expectation-related processing has provided convincing evidence for the reduced neural processing of expected sensory inputs, indicating a predictive coding mechanism in perceiving sensory information (Alink et al., 2010; den Ouden et al., 2010; Kok et al., 2012; Kok and de Lange, 2015; Murray et al., 2002). Results of Study 2 and 3 are in line with these findings, suggesting increased predictive processing of voluntary action outcomes than for externally-generated sensory stimuli.

Analysis on detection-related BOLD activity revealed no significant effects for detected compared with undetected trials. However, there was relative involvement in a number of areas depending on the specific movement and modality, and an interaction between the two factors. First, increased BOLD activity was found in the cerebellar vermis for voluntary compared with externally-generated movements. The cerebellum has been proposed as an area where forward models are computed, and has been demonstrated to integrate sensory inputs from different sensory modalities as well as from efference copy signals (Baumann et al., 2015; Imamizu, 2010). More specifically, this area has been shown to play a role in modulating the sensory consequences of motor commands and providing error signal for the unexpected consequences of these commands (Blakemore et al., 2001; Blakemore et al., 1998; Blakemore and Sirigu, 2003; Leube et al., 2003a; Miall et al., 1993). This area has also been found to provide timing information for motor as well as non-motor processes (Baumann et al., 2015; Ivry, 1996; Ivry and Richardson, 2002). The finding of increased involvement in the cerebellum regarding detection-related activity in voluntary compared with externally-generated condition suggests that this area was specifically implicated in the perception of temporal discrepancies for voluntary action outcomes, and provides further support for the differential involvement of cerebellar areas in generating internal predictions about the sensory outcomes of voluntary actions (Blakemore et al., 2001; Blakemore et al., 1999; Blakemore and Sirigu, 2003; Wolpert et al., 1998).

Additional findings regarding detection-related BOLD activity concern multisensory interactions. Accordingly, detection-related BOLD activity in unimodal trials engaged the right MTG and the right occipital cortex more than in bimodal trials. Research on multisensory processing has provided substantial evidence for enhanced behavioral performance (i.e., heightened perceptual awareness, decreased reaction times) coupled by increases in cortical activity linked to sensory processing (Driver and Spence, 2000; Shimojo and Shams, 2001). In addition, there is evidence that such enhancement can also be observed even when a stimulus provides no information about the other sensory modality (Foxe et al., 2000; Giard and Peronnet, 1999; Lovelace et al., 2003; McDonald et al., 2000; Stein et al., 1996; Vroomen and de Gelder, 2000). On the other hand, just as a particular sensory modality can enhance the processing of another modality, it can also hinder its processing (Colavita, 1974; Laurienti et al., 2000; Macaluso et al., 2000; Sinnett et al., 2008). For example, Laurienti et al. (2000) found significant reductions in cortical activity linked to visual processing during the presentation of auditory inputs and vice versa, possibly as a way of increasing the salience of the relevant sensory modality that is presumably more important in the processing hierarchy. In both cases, spatiotemporal correspondences as well as semantic congruencies between different sensory inputs seem to drive these effects (Murray et al., 2004; Senkowski et al., 2008). When considered in light of these findings, increased activity in the right temporal and occipital areas indicate that the additional auditory modality in Study 3 inhibited, at least partly, the processing of temporal information. In other words, it seems that even though the auditory stimulus provided timing information about the visual feedback, it was not *used* for the behavioral task. Another area in the posterior cerebellum, namely the left cerebellum lobule VIII was also implicated more during unimodal than during bimodal trials. Moreover, the cerebellum lobule VIII, though with a different peak activation, has also been found to be more involved for voluntary movements with unimodal outcomes than with bimodal outcomes. This supports the assumption of inhibition regarding the presentation of auditory stimulus specifically when the movement was voluntary. All together, these results indicate an inhibitory mechanism being at work for the additional auditory modality linked with the voluntary movement execution, even though it carried valuable information about the timing of the visual feedback. In this respect, findings of Study 3 raise the possibility that auditory stimulus was not perceived as part of the movement, as it consisted of a beep that have made it difficult to be perceived as arising from the movement. Technical limitations preventing more complex auditory stimuli to be presented without an additional unwanted delay were the reason why beeps were chosen as auditory stimuli. In our future experiments, the aim is to include more ecologically valid auditory stimuli to investigate multisensory interactions during the processing of action outcomes.

On a behavioral level, higher proportion of delay responses were found for externally-generated compared with voluntary movements. Decreased proportion of delay detection in the voluntary movement condition suggests that these movements and their effects might have been perceived as closer in time, suggesting intentional binding effects (Haggard et al., 2002). On the other hand, despite these findings, a recent study showed an opposite pattern regarding the perceptual delay judgments for voluntary vs. externally-generated movements and their effects (van Kemenade et al., 2016). Accordingly, delay responses to self-generated button presses and their outcomes were significantly higher than when the button was pressed down automatically. These seemingly contradictory results might be attributed to the difference between movement-related (i.e., feedback occurs during movement, as in the present study) and outcome-related (i.e., feedback occurs at the end of movement, as in the previous study) feedback. This distinction, also referred to as the distinction between proximal and distal outcomes (Metcalfe et al., 2013) has recently attracted attention, and was investigated with regard to sense of agency (David et al., 2016; Metcalfe et al., 2013). Differences in behavioral responses in Study 2 and 3 might reflect this difference in processing of movement vs. outcome-related feedback.

Despite these novel findings, one limitation in Study 3 concerns potential differences in movement kinematics within and across voluntary and externally-generated movements. In the present study, movement range was restricted by the PMD, and participants were trained prior to the fMRI experiment and their movements were monitored constantly throughout the fMRI experiment. In addition, movement recordings taken from 18 participants were tracked to check compliance with instructions, and no significant differences in the average movement duration across movements were found. Nevertheless, it should be kept in mind that kinematics of voluntary movements could have been more variable than that of externally-generated movements, and that might have influenced the results.

Although action outcome processing has been extensively investigated, studies using realistic sensory feedback of the action are limited. A recent study by Benazet et al. (2016) focused on this important factor by using visual feedback of a moving limb. In line with results of Study 3, they found that cortical processing of visual re-afferent signals are suppressed, but only when the signals are correctly predicted. Integrating real world situations to experimental paradigms is of crucial importance, and more studies are needed for investigating realistic action outcome relations. In addition, recent investigations have found contradictory evidence for the reduced sensation and neural processing of voluntary action outcomes (Reznik et al., 2015, 2014; Roussel et al., 2013; Yon and Press, 2017). Therefore, more studies are needed to clarify mechanisms involved in perceiving sensory outcomes of voluntary movements, whether and how differential predictive processing for these movements exist, as well as the impact of multisensory processing on action outcome prediction.

In conclusion, action-related predictive processes for voluntary movements leading to unimodal vs. bimodal consequences were for the first time investigated using an ecologically-valid set up. Externally-generated movements allowed for effectively distinguishing the influence of efference copy-related processes from re-afferent feedback. Suppressed BOLD responses were found in somatosensory, visual and auditory processing areas for voluntary compared with externally-generated movements, and during the presentation of both feedback modalities, indicating multisensory predictive mechanisms. Subjective detection of delays were found to be linked with increased cerebellar processing for voluntary movements, and additionally for voluntary movements with unimodal visual feedback. Unimodal visual trials were also accompanied by increased activity in areas associated with visuo-motor processing, indicating multisensory influences in detection-related BOLD activity. Together, these findings extend previous accounts regarding BOLD suppression to a well-controlled realistic context. Furthermore, these results support the relevance of cerebellum in processing error-related temporal information for voluntary action outcomes, and highlight the importance of investigating multisensory influences on action outcome processing.

6 GENERAL DISCUSSION

6.1 Summary of the main findings

The aim of the present dissertation was to investigate behavioral and neural indices of perceiving multisensory action outcomes. Accordingly, distinctive processing of action outcomes have been examined in two domains: distortions in time perception for multisensory inputs triggered by voluntary movements and neural correlates of perceiving unimodal vs. bimodal action outcomes.

In Study 1, perception of synchrony for multisensory stimulus pairs triggered by voluntary or externally-generated button presses was assessed. In addition, the influence of temporal contiguity between the movement and its multisensory outcome on perceived synchrony for these outcomes was examined. Results provided evidence for widened window of subjective simultaneity for AV stimulus pairs when action outcome associations were time-congruent. Inclusion of delays between the action and the AV outcome, corresponding to decreased temporal contiguity, narrowed the WSS. In other words, participants became more sensitive to asynchronies between auditory and visual inputs when these inputs occurred further away in time from the voluntary movement. However, the effect of delay on simultaneity perception was not proportional to the amount of delay, as found in Study 1.1. Accordingly, delays of 417.5 and 2500ms had a similar impact on SJs, suggesting that the effect might saturate after about 400ms. Similarity of SJs across voluntary and externally-generated movements in Study 1.2 points to a causal influences on time perception for multisensory stimulus pairs associated with these movements. In Study 1.2 simultaneity judgments were found to be similar across voluntary and externally-generated movements, with widened WSS around action time narrowing as delays increased. However, voluntary and externally-generated movements differ with regard to the slopes of SJ curves, with significantly steeper slopes for voluntary in comparison with externally-generated movements. This findings speaks for distinctive precision in judgments of synchrony for sensory inputs associated with voluntary movements.

In Study 2, neural correlates of perceiving voluntary movements with unimodal vs. bimodal outcomes were examined. For this purpose, unimodal visual or auditory as opposed to bimodal AV stimuli triggered by voluntary button presses were compared with similar sensory stimuli that were presented after a cue (passive viewing). Delays ranging from 0 to 417ms were introduced between the button press and the sensory outcome in order to assess how temporal discrepancies concerning the action outcome relation were processed in the brain, and whether modality of the outcome to be reported and whether there was additional sensory modality would influence error-related processing of action outcomes. Findings suggest BOLD suppression in visual, auditory and somatosensory areas of the brain when sensory stimuli were triggered by voluntary movements compared with when they were passively perceived. Interestingly, these areas were suppressed both during unimodal and bimodal trials, pointing to predictive processing of equally likely action outcomes. Moreover, suppression effects were observed for all modalities to be reported, suggesting similar perceptual processing of different sensory stimuli triggered by voluntary movements. Detection-related BOLD responses were found to differ depending on the sensory outcome, with cerebellar areas recruited for movements leading to bimodal outcomes, speaking for multisensory advantage for detecting sensorimotor discrepancies in the action outcome relation.

In Study 3, neural correlates of perceiving multisensory action outcomes were investigated using realistic feedback of the hand. In addition, contrasting voluntary with externally-generated actions made it possible to effectively distinguish the influence of efference copy-related predictive processing from re-afferent feedback, and address action-specific processes on perceiving sensory outcomes of these actions. Participants performed hand movements themselves or with the use of the PMD as they saw visual feedback of their hand movements in real time or with delays. They were asked to detect delays between their actual movement and its visual outcome. Half of the trials contained auditory beeps coupled to the onset of the visual outcome that would presumably provide additional temporal information for the detection task. Results provided support for BOLD suppression as demonstrated by reduced BOLD responses in somatosensory, visual and auditory processing areas for voluntary compared with externally-generated movements. BOLD suppression in these areas was again similar for both unimodal and bimodal conditions, pointing to multisensory predictive mechanisms. Detection of delays modulated BOLD responses in the cerebellar vermis differentially for voluntary compared with externally-generated movements, supporting the involvement of this area in sensorimotor prediction. Moreover, activity in the cerebellar lobule VIII was higher for voluntary movements with unimodal outcomes, and unimodal trials in general were associated with higher involvement of areas linked with visuo-motor processing (temporo-parietal areas and cerebellum lobule VIII), suggesting inhibition in processing the additional modality, at least at a neural level.

Together, findings of the present dissertation refine our understanding of *what* is distinct about perceiving voluntary action outcomes, with the aim to reconcile the role of multisensory processing on action outcome perception that has so far been overlooked. In this respect, results of the present dissertation provide support for the predictive processing of voluntary actions and their outcomes, and extend it to multisensory action outcomes. These points are discussed in the following sections.

6.2 Multisensory influences on action outcome processing

Despite substantial evidence on interactions among different sensory modalities, research on the interplay between voluntary actions and multisensory processing is scarce. Research on multisensory perception has provided support for behavioral enhancement (Arabzadeh et al., 2008; Bresciani et al., 2008; Diederich and Colonius, 2004; McDonald et al., 2000; Teder-Sälejärvi et al., 2005) as well as inhibition (Colavita, 1974; Meredith, 2002; Morein-Zamir et al., 2003; Sinnett et al., 2008; Wang et al., 2012). Moreover, several studies demonstrated that multisensory processing in the brain begins in early stages, contrary to once assumed, and in areas previously thought to be modality specific (Driver and Spence, 2000). Importantly, temporal and spatial correspondences as well as semantic congruencies seem to modulate multisensory enhancement/inhibition (Calvert et al., 2000; Murray et al., 2004; Senkowski et al., 2007).

Study 1 of the present dissertation provided evidence that asynchronies between multiple sensory inputs associated with a voluntary movement are tolerated. Concerning voluntary actions, recent investigations have demonstrated a tendency to perceive sensory modalities as simultaneous if they are thought to be associated with a voluntary movement (Corveleyn et al., 2015; Desantis and Haggard, 2016a, 2016b; Parsons et al., 2013). In addition, the assumption that the action leads to a sensory outcome aids in intentional binding between the action and the outcome, which in turn would contribute to the assumption that sensory signals from different modalities belong to the action, the so-called unity assumption (Rohde et al., 2014; Vatakis and Spence, 2008, 2007; Welch and Warren, 1980). Concerning Study 1 of the present dissertation, increased simultaneity responses for AV stimuli triggered by voluntary button presses presumably help maintain coherent perception of an event as a whole. In Study 2, behavioral detection performance was found to be increased for bimodal than for unimodal action outcomes, speaking for multisensory enhancement. On the contrary, findings of Study 3 suggest no behavioral enhancement. This might have arised from the fact that the auditory stimulus was not perceived as part of the movement, even though it provided timing information between the action and the visual outcome. As stated previously, it is not just temporal and spatial correspondences that determine multisensory enhancement or inhibition, but also the semantic congruency between sensory signals that modulate cross-modal interactions (Calvert et al., 2000; Murray et al., 2004; Senkowski et al., 2007). The brain not only combines sensory information, nor it always compensates for neural and physical differences in processing times across sensory modalities, it also attributes different sources to different sensory inputs (Ernst and Bülthoff, 2004; Shams and Beierholm, 2010; Welch and Warren, 1980). In fact, sensory inputs originating from different sources need to be segregated (Gau and Noppeney, 2016). Spatiotemporal and semantic correspondences provide cues to solve the issue of integration/segregation (Doehrmann and Naumer, 2008; van Atteveldt et al., 2014; Wallace et al., 2004). Regarding the lack of behavioral effects found in Study 3, it could be argued that semantic correspondences might have provided the cue to discern whether different sensory stimuli occurring around the same time originated from a common or different source. Although a direct conclusion on multisensory integration/segregation cannot be made concerning the results of the present dissertation, it seems that overall, different sensory modalities presented together in Study 1 and 2 point to an increased tendency to integrate them to the action, whereas auditory stimulus in Study 3 suggest the opposite tendency to segregate it from the visual outcome of the movement. A direct examination of multisensory integration/segregation concerning voluntary actions provides valuable insights into how humans attribute common or separate causes to sensory events occurring around them, and infer agency over them or an outside source. Such information carries high survival value to the organism (Gau and Noppeney, 2016).

As regards neural correlates of multisensory action outcome processing, results of Study 2 and 3 showed that equal likelihood of unimodal and bimodal outcomes associated with voluntary movements lead to BOLD suppression in not only somatosensory and visual, but also auditory areas of the cortex. In other words, the expectation that the movement might lead to unimodal and bimodal outcomes resulted in suppressed BOLD responses for the additional modality specifically for voluntary movements. On the other hand, findings concerning detection-related activity in Study 2 and 3 suggest that multisensory information is processed differently in cases where temporal discrepancy was detected, with recruitment of areas of the posterior cerebellum, supporting cerebellum’s role in sensorimotor prediction and integration (Blakemore et al., 2001, 2000; Blakemore et al., 1998; Blakemore and Sirigu, 2003; Synofzik et al., 2008; Wolpert et al., 1998). In addition, semantic congruency of sensory stimuli seem to modulate accompanying cerebellar processing with regard to perceived temporal discrepancies between the movement and the outcome. Study 2 demonstrated increased involvement of the cerebellum for bimodal action outcomes, in which voluntary button presses triggered the occurrence of a dot and a tone. However, in Study 3, realistic visual outcome of the hand movement was accompanied by auditory beeps during bimodal trials. Results showed increased involvement of the cerebellar lobule VIII for voluntary movements with only visual outcome than with bimodal outcome, suggesting interference by the additional auditory modality in processing action-related discrepancies at a neural level. However, due to lack of behavioral differences in delay detection across unimodal and bimodal trials, results of Study 3 must be interpreted with caution. Nevertheless, these findings provide new evidence for multisensory influences in perceiving voluntary action outcomes, both on a neural as well as behavioral level.

6.3 What is unique about voluntary actions? Perceptual experience and accompanying neural responses regarding voluntary action outcomes

Sensory outcomes of voluntary actions have been proposed to be distinctively perceived compared with sensory outcomes produced externally. According to the forward model framework, an efference copy of the motor command informs the system about the predicted sensory consequences of voluntary movements (Wolpert et al., 2001; Wolpert et al., 1995; Wolpert and Ghahramani, 2000). A match between the actual and the predicted outcome of the movement results in suppressed sensation for the outcome. A mismatch informs the system about changes in the environment or state estimation, which leads to updating of predictions (Miall et al., 2007; Wolpert et al., 2001; Wolpert and Kawato, 1998). Such predictive processing presumably aids in efficient detection of unexpected or salient inputs and sense of control over events (Blakemore et al., 2000; Moore and Obhi, 2012; Pynn and DeSouza, 2013; Tsakiris et al., 2005). Sensory suppression and distorted time perception for action outcomes (i.e. intentional binding) are thought to be the results from forward action models (Bays et al., 2005; Haggard et al., 2002; Voss et al., 2008; Wolpert et al., 1995; Wolpert and Kawato, 1998). In addition, suppressed responses are found to be correlated with decreased BOLD activity in sensory cortices, with recruitment of areas such as the cerebellum, angular gyrus and ACC in the case of discrepancy between the predicted and actual sensory outcome associated with the action (Blakemore et al., 2001, 2000; Blakemore et al., 1999; Blakemore et al., 1998; Blakemore and Frith, 2003; Farrer et al., 2008; Krieghoff et al., 2011, 2009). Results of the present dissertation provide support for the forward model explanation. For example, Study 1.2 showed that voluntary movements lead to increased precision for synchrony judgments compared with externally-generated movements, which is in line with the assumption that predictive processing of voluntary action outcomes lead to distinctive sensory experience for these outcomes. Study 2 and 3 demonstrated BOLD suppression in sensory cortices for expected outcomes of voluntary actions, supporting previous findings on sensory suppression at a neural and behavioral level (Bays et al., 2006, 2005; Benazet et al., 2016; Blakemore et al., 1999; Voss et al., 2008). It also extends these findings to multisensory inputs. Despite this, a number of studies provided contradictory evidence regarding reduced sensation and neural processing of self-generated action outcomes (Reznik et al., 2015, 2014; Roussel et al., 2013; Yon and Press, 2017). Therefore, more studies are needed to clarify mechanisms involved in perceiving sensory outcomes of intentional movements, as well as multisensory influences in this process.

Study 2 and 3 also indicated specific involvement of cerebellar structures in perceiving error-related information regarding voluntary actions and their outcomes. However, it should also be kept in mind that cerebellum is also involved in temporal processing (Harrington and Peck, 1998; Ivry et al., 2002; Ivry and Keele, 1989; Koch et al., 2007). Regarding the specific role of the cerebellum in action-perception, Leube et al. (2003a) suggested that this area is more involved in timing perception of visual events. In an attempt to uncover the contribution of the cerebellum in sensorimotor vs. time processing, Block and Bastian (2012) found activity in cerebellar structures with motor, but not sensory adaptation, pointing to particular involvement of this area for motor-related activity. Nevertheless, results of Block & Bastian (2012) is far from being conclusive. Therefore the specific involvement of this area in perceiving action outcome discrepancies need to be clarified in future studies.

6.4 What might be *not* unique about voluntary actions? The influence of causality, predictability, and expectations

While the dominant view in the study of action perception involves the assumption that a unique association exists for voluntary actions and their sensory outcomes, mostly through predictive mechanisms acquired via learning (Hughes et al., 2012; Prinz, 1997; Rizzolatti et al., 2010; Waszak et al., 2005; Wolpert et al., 1995), recent approaches have also pointed out factors other than action-specific mechanisms that influence action outcome processing (Buehner, 2012; Buehner and Humphreys, 2009b; Kok and de Lange, 2015; Parsons et al., 2013; Roussel et al., 2013; Summerfield et al., 2008). These comprise predictability, causality and stimulus expectation.

The first factor concerns the role of predictability. In an attempt to scrutinize action specific processes, Hughes et al. (2012) pointed out that temporal prediction, defined as the ability to predict the occurrence of a stimulus in time, might be present for externally-generated stimuli as well, and therefore is not specific for voluntary action outcomes. Non-motor identity prediction, prediction regarding the identity of the stimulus, might also be present in cases where no action precedes the stimulus (Hughes et al., 2012). What is unique about intentional actions is the fact that stimulus followed by the action can be precisely predicted in time through motor control mechanisms (temporal control), and also that the specific action effect can be predicted (motor-identity prediction). In support of this, auditory N1 attenuation has been shown to occur only for action effects that were congruent with predictions (Hughes et al., 2013). Such investigations necessitate the inclusion of different baseline conditions to be able to infer the contribution of temporal prediction, non-motor identity prediction, motor identity prediction and motor control (Hughes et al., 2012). In the present dissertation, baseline conditions in all studies were designed to reflect the real world situations where externally-generated sensory inputs cannot be predicted in time.

This allowed for a more naturalistic representation of these stimuli. On the other hand, it had the disadvantage that temporal prediction might have influenced the results. Future studies would benefit from a more thorough examination of temporal prediction, temporal control, non-motor as well as motor-identity prediction on action outcome processing.

Second issue in studying action specific processes is related to the role of causality. Accordingly, causal beliefs about the components of an event seem to drive our perceptual experience which in turn might influence action outcome perception (Buehner, 2012; Buehner and Humphreys, 2009b; Eagleman and Holcombe, 2002; Parsons et al., 2013). For example, Buehner and Humphreys (2009b) demonstrated intentional binding for events not associated with a voluntary action. Study 1 of the present dissertation provides supporting evidence for the role of causality, demonstrated by the finding that asynchronies between different sensory modalities are tolerated around an action, no matter whether the action was voluntary or not. Nevertheless, the results also showed increased precision in judgments of simultaneity only for voluntary movements, pointing to action specific processing of sensory stimuli. Still, findings of Study 1 highlight the importance of distinguishing between factors such as causality, which might affect conclusions driven about action specific processes.

Third factor that needs to be considered is the impact of expectations. It has been found that neural processing of expected sensory stimuli are reduced (Kok et al., 2012; Kok and de Lange, 2015; Murray et al., 2002). This suggests a predictive coding mechanism in perceiving sensory information, which might not associated with a voluntary action. In this respect, equal likelihood of unimodal and bimodal outcomes associated with voluntary actions in Study 2 might be responsible for the reduced neural responses, instead of sensory suppression effects. However, similar findings were present in Study 3, when the baseline condition would allow for a more specific inference regarding predictive processing of action outcomes. Still, a direct conclusion regarding expectation-related processing cannot be made, as the paradigm in Study 3 was not suited to test such a question. On the other hand, recent investigations by Reznik et al. (2015, 2014) suggest that neural and behavioral suppression might not as simple as a general reduction for the processing of the action-related sensory input, and rather depend on the expectation about stimulus intensity (Reznik et al., 2015, 2014). Indeed, the researchers found that auditory action outcomes can enhance sensory processing areas, depending on the task at hand. Other investigations have supported the view that the timeline of sensory suppression might not as straightforward as it was previously considered (Ackerley et al., 2012; Hughes and Waszak, 2011; Simões-Franklin et al., 2011). Although findings of the present dissertation rather support the traditional view of sensory suppression, results concerning suppressed BOLD responses in sensory cortices, along with the results showing BOLD suppression for all likely outcomes might be influenced by expectation related processing. Future studies should look into the role of expectations on voluntary action outcome processing.

To sum up, a number of factors other than action effect prediction has been demonstrated to affect how voluntary action outcomes are perceived. These involve predictability, causality and stimulus expectation. Effective control of these factors in experimental paradigms would extend our understanding of voluntary action perception, and of other factors important in understanding how we interact with the world around us.

6.5 Conclusions and Outlook

In this doctoral thesis, behavioral and neural indices of perceiving multisensory action outcomes have been investigated. The findings support distinctive processing of sensory inputs associated with voluntary actions, and provide new evidence concerning multisensory influences on how action outcome associations are processed. These findings are in line with the view that predictive processing of learned associations between voluntary actions and their sensory effects are responsible for the distinctive experience. However, they also emphasize the role of causality, predictability and expectations in modulating how action effects are perceived.

Apart from understanding mechanisms behind sensorimotor learning and integration, research on action outcome perception provides invaluable information on agency deficits observed in patients with schizophrenia. Delusions of control commonly observed in patients with schizophrenia has been linked to misattribution of sensory outcomes produced by the self to an external source (Ford et al., 2014; Ford and Mathalon, 2005; Frith, 2012; Pynn and DeSouza, 2013; Synofzik et al., 2010). Indeed, many positive symptoms of schizophrenia are thought to reflect aberrant prediction and monitoring of sensory inputs triggered by the self (Frith, 2012). In line with this assumption, several studies found that patients with schizophrenia, specifically those who experience hallucinations and passivity symptoms, exhibit reduced tendency to suppress the sensory outcomes of their own movements (Backasch et al., 2014; Blakemore, 2003; Blakemore et al., 2000; Shergill et al., 2005). Apart from schizophrenia, deficits in integrating sensory and motor signals as well as predicting the next state of the system have been implicated in dyslexia and autism (Blau et al., 2009; Ross et al., 2007; Stekelenburg et al., 2013). Future studies focusing on the psychophysiological and neural basis of these disorders would benefit immensely from incorporating multisensory processing and voluntary actions.

Another implication concerns interventions aimed at improving the daily life of patients having difficulties in sensorimotor processing due to stroke, limb amputation or spinal cord injury (Collins et al., 2017; Johansson, 2012). Accordingly, the conscious experience of owning of one's body parts, referred to as body ownership, has been proposed to depend on the integration of multiple bodily sensations such as touch, proprioception and vision (Botvinick, 2004; Botvinick and Cohen, 1998; Ehrsson et al., 2004). Although voluntary actions have been found to boost body ownership through predictive processing of sensory inputs (Tsakiris et al., 2010), the relation between body ownership and voluntary movements seems to be an intricate one, as revealed by heterogeneous findings (Kalckert and Ehrsson, 2014, 2012; Kammers et al., 2009; Tsakiris et al., 2010; Walsh et al., 2011). Unraveling the link between one's own bodily self and sense of control over events would lead the way to the development of effective intervention techniques, as shown by a number of investigations (Alimardani et al., 2013; Collins et al., 2017; Ehrsson et al., 2008; Moseley et al., 2008).

In sum, findings of the present dissertation extend our knowledge on action outcome processing to multisensory action outcomes by providing novel insights on how sensory modalities associated with voluntary movements are perceived and processed in the brain.

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8 APPENDIX

Table I. Anatomical locations of common peak activations for voluntary movements with unimodal and bimodal outcomes (conjunction: [($Pas_{Uni}Vis > Vol_{Uni}Vis$) ∩ ($Pas_{Uni}Aud > Vol_{Uni}Aud$) ∩ ($Pas_{Uni}AV > Vol_{Bi}Vis$) ∩ ($Pas_{Uni}AV > Vol_{Bi}Aud$)]). Significance level: $pFWE < .05$, cluster with at least 5 voxels.

Anatomical Region	**Cluster Extent**	**Coordinates**					**no. Voxels**
		Hem.	***x***	***y***	***z***	**T-value**	
PCG	PRG, IPL	Left	-36	-24	-52	13.38	1209
	Heschl's gyrus, RO	Left	-46	-24	8	10.01	891
	STG, Heschl's gyrus, RO	Left	-40	-30	12	9.46	
Occipital cortex	Calcarine, LG	Right	18	-98	-4	9.95	1134
		Right	20	-96	-4	12.43	
	MOG	Right	28	-92	0	9.61	
	IOG	Right	36	-82	-10	7.64	
Occipital cortex	IOG, calcarine gyrus	Left	-22	-94	-2	9.81	788
STG	Supramarginal gyrus, MTG	Right	64	-28	10	9.55	1263
	Heschl's gyrus, RO	Right	52	-20	8	8.75	
SMA	MCC	Left	-6	-4	54	8.98	692
	SMA, SFG	Right	8	6	56	6.26	
	SMA, SFG	Right	10	2	64	5.71	
Cerebellum	V 56%, FG	Right	16	-50	-20	7.22	369
	VI 84%, FG	Right	28	-44	-28	6.18	
	VI 97%, FG	Right	28	-52	-24	6.08	
IFG	IFG pars Tri./pars oper.	Right	42	8	28	7.11	236
Cerebellum	VIIIa (Hem.) 33%, VIIIb (Hem.) 24%	Right	22	-60	-48	6.94	79
	VIIIa (Hem.) 60%	Right	30	-54	-50	4.99	
Insula	IFG pars Tri./pars oper.	Right	34	22	8	5.62	25
Thalamus	Pallidum	Left	-10	-18	4	5.44	89
MCC	PCC		0	-40	36	5.21	22

Coordinates are listed in MNI space. FG: fusiform gyrus; IFG: inferior frontal gyrus; IOG: inferior occipital gyrus; IPL: inferior parietal lobule; LG: lingual gyrus; MCC: middle cingulate cortex; MOG: middle occipital gyrus; MTG: middle temporal gyrus; PCC: posterior cingulate cortex; PCG: postcentral gyrus; PRG: precentral gyrus; RO: rolandic operculum; SFG: superior frontal gyrus; SMA: supplementary motor area.

Table II. Processing of subjectively delayed and undelayed trials (p < .001 uncorrected, cluster extent: 50 voxels)

Anatomical Region	Cluster Extent			Coordinates			no. Voxels	*P* peak
		Hem	***x***	***y***	***z***	**T-value**		**FWE**
PH	HC	Left	-30	-34	-12	5.58	1925	.003
	Putamen, pallidum, insula	Left	-28	-2	-2	5.16		.017
	HC, amygdala	Left	-22	-16	-12	4.72		.083
Precuneus		Right	14	-60	22	5.53	3807	.004
	Precuneus	Left	-4	-62	18	4.79		.065
	Calcarine gyrus	Left	-6	-56	4	4.69		.092
MTG	ITG, TP	Right	64	-6	-20	5.16	170	.017
	MTG, STG	Right	60	-12	-16	4.61		.119
MTG	STG, ITG	Left	-60	-8	-18	4.93	616	.039
	MTG, STG, ITG	Left	-64	-20	-8	4.54		.151
	TP	Left	-46	10	-34	4.32		.293
Calcarine gyrus	IOG, MOG	Left	-16	-96	-6	4.76	766	.073
	LG	Left	-24	-86	-14	4.28		.328
	FG	Left	-32	-80	-14	3.76		.855
MFG	SFG, MFG	Right	32	44	42	4.62	80	.117
	MFG, rectus		0	48	-12	4.49	1005	.176
	MFG	Left	-4	58	-4	4.27		.336
	ACC	Left	-4	38	-6	3.93		.694
IOG	LG, FG	Right	30	-90	-16	4.48	183	.184
	Calcarine gyrus, LG	Right	12	-98	-6	3.68		.91
Angular gyrus	MOG, IPL	Right	50	-68	32	4.46	178	.20

Anatomical Region	**Cluster Extent**	**Coordinates**					**no. Voxels**	***P* peak**
		Hem	***x***	***y***	***z***	**T-value**		**FWE**
Putamen	Pallidum, amygdala	Right	28	0	-6	4.42	1034	.22
	HC, ParaHC, FG	Right	34	-30	-10	4.38		.25
	Putamen, insula, pallidum	Right	34	-6	-6	4.21		.39
STG	MTG, RO	Right	60	-28	8	4.37	81	.25
	STG, Heschl's gyrus, RO	Right	54	-22	6	3.27		1.00
TP	ITG	Right	48	16	-32	4.29	54	.32
	ITG, MTG, TP	Right	52	4	-36	3.22		1.00
MFG	Precentral gyrus, IFG	Left	-38	20	46	4.23	116	.37
SFG	Medial SFG, MFG	Left	-12	58	36	4.16	189	.44
	mSFG, SFG	Left	-10	66	24	3.80		.83
	mSFG	Left	-8	48	50	3.46		.99
LG	Cerebellum, PH	Right	18	-36	-12	4.02	209	.59
	LG, FG, PH	Right	24	-50	-8	3.80		.82
	Vermis, LG	Right	2	-30	-10	3.19		1.00
ITG	FG, cerebellum	Right	44	-48	-24	4.00	53	.62
PCG	PRG, SPL	Left	-28	-32	76	3.97	462	.65
	PCG, SPL, precuneus	Left	-24	-38	66	3.84		.78
	Paracentral gyrus, PCG, PRG	Left	-12	-30	82	3.77		.84
STG	MTG, SMA	Left	-56	-32	12	3.88	71	.75
MTG	STG, ITG	Right	48	-70	8	3.86	120	.77

Anatomical Region	Cluster Extent	Coordinates					no. Voxels	*P* peak
		Hem	***x***	***y***	***z***	**T-value**		**FWE**
	MOG, MTG, IOG	Right	40	-72	0	3.40		.99
MTG	STG, RO	Left	-46	-40	6	3.66	83	.92
	MTG, RO, Heschl's gyrus	Left	-40	-36	16	3.65		.93
	MTG, STG, ITG	Left	-48	-48	6	3.47		.99
MOG	Angular gyrus, IPL	Left	-44	-74	34	3.45	68	.99
	Angular gyrus, MOG, MTG	Left	-44	-66	24	3.40		.99
	Angular gyrus, MOG, IPL	Left	-40	-70	40	3.21		1.00

Coordinates are listed in MNI space. ACC: anterior cingulate cortex; FG: fusiform gyrus; IFG: inferior frontal gyrus; IPL: inferior parietal lobule; IOG: inferior occipital gyrus; ITG: inferior temporal gyrus; LG: lingual gyrus; MOL: medial occipital lobe; MOG: middle occipital gyrus; MFG: medial frontal gyrus; MTG: middle temporal gyrus; PCG: postcentral gyrus; PG: parahippocampal gyrus; PRG: precentral gyrus; RO: rolandic operculum; SFG: superior frontal gyrus; SOG: superior occipital gyrus; SPL: superior parietal lobule; STG: superior temporal gyrus; TP: temporal pole.

Table III. Anatomical locations of common peak activations for voluntary and externally-generated movements (pFWE < 0.05).

Anatomical Region	Coordinates					
	Hem.	***x***	***y***	***z***	**T-value**	**no. Voxels**
Inferior occipital gyrus	Left	-36	-88	-8	15.5	2506
Middle occipital gyrus	Left	-46	-80	0	13.2	
Calcarine fissure	Left	-14	-94	-6	12.7	
Middle occipital gyrus	Right	36	-90	2	15.05	2845
Calcarine fissure	Right	20	-96	-4	12.43	
Inferior occipital gyrus	Right	46	-78	-6	11.41	
Postcentral gyrus	Right	48	-24	52	10.48	749
Postcentral gyrus	Right	52	-20	46	9.52	
Postcentral gyrus	Right	32	-36	46	6.17	
Postcentral gyrus	Left	-44	-32	46	9.68	1380
Inferior parietal lobule	Left	-52	-26	48	8.58	
Supramarginal gyrus	Left	-56	-22	42	8.21	
SMA	Left	0	2	56	7.65	280
Inferior frontal gyrus, opercular part	Right	54	10	30	6.87	485
Inferior frontal gyrus, opercular part	Right	52	12	4	6.15	
Insula	Right	40	20	2	5.67	
Thalamus	Left	-14	-18	6	6.49	115
Thalamus	Left	-16	-26	-2	5.11	
Supramarginal gyrus	Right	64	-34	24	6.32	76
Insula	Left	-34	18	4	6.16	75
Fusiform gyrus	Right	38	-72	-20	6.15	1
Rolandic operculum	Left	-46	-2	8	6.03	50
Cerebellum VIII	Left	-20	-66	-50	5.45	78
Rolandic operculum	Right	56	-22	22	5.03	11

Table IV. Anatomical locations of peak activations for externally-generated vs. voluntary movements (Ext > Vol contrast) ($pFWE < 0.05$).

Anatomical Region	Coordinates					no. Voxels
	Hem.	*x*	*y*	*z*	T-value	
Rolandic operculum	Left	-44	-22	32	8.68	1703
STG	Left	-54	-46	16	6.44	
Supramarginal gyrus	Left	-52	-38	30	6.18	
Supramarginal gyrus	Right	52	-32	24	6.76	766
STG	Right	48	-40	10	5.39	
SMA	Left	-6	6	56	6.57	1657
SMA	Right	8	2	50	6.07	
Middle frontal gyrus	Left	-24	26	44	5.86	
Insula	Right	30	24	8	6.19	155
Precentral gyrus	Left	-54	2	16	6.14	92
Putamen	Left	-24	4	4	6.11	432
Insula	Left	-28	22	4	5.79	
Putamen	Left	-24	16	-4	5.38	
Postcentral gyrus	Left	-22	-42	60	5.8	297
Postcentral gyrus	Left	-34	-34	58	5.76	
Precentral gyrus	Left	-20	-24	68	4.98	
Precentral gyrus	Left	-36	-14	56	.578	34
MTG	Left	-48	-64	22	5.56	174
MTG	Left	-42	-66	8	5.33	
Paracentral lobule	Left	-6	-24	52	5.52	321
SMA	Right	8	-18	48	5.19	
Precuneus	Right	6	-56	34	5.35	281
Precuneus	Right	6	-64	26	5.19	
Precuneus	Right	16	-62	28	5.17	

Anatomical Region	Coordinates					no. Voxels
	Hem.	*x*	*y*	*z*	T-value	
Anterior cingulate cortex	Right	10	22	26	5.35	51
Putamen	Right	22	10	8	5.24	21
Paracentral lobule	Right	12	-36	58	5.22	51
Putamen	Right	26	-2	10	5.18	18
MTG	Right	46	-62	8	5.17	26
Postcentral gyrus	Right	24	-40	58	5.16	34
Middle occipital gyrus	Right	40	-70	6	5.11	15
Superior occipital gyrus	Left	-22	-74	30	5.09	13
Superior frontal gyrus	Left	-24	-6	62	5.08	12
Middle frontal gyrus	Right	38	-4	52	5.06	4
Superior frontal gyrus, medial	Right	2	40	40	5.04	74
Superior occipital gyrus	Left	-18	-66	38	5.03	21
Precuneus	Right	16	-58	48	5.02	16
Thalamus	Right	4	-26	-4	5.01	16
Thalamus	Left	-4	-26	-2	4.84	
Middle cingulate gyrus	Left	-2	-42	44	4.93	8
IPL	Left	-50	-58	40	4.93	5
Middle frontal gyrus	Right	28	42	14	4.92	7
Angular gyrus	Left	-36	-52	34	4.91	6
Precuneus	Left	-14	-58	48	4.88	4
Angular gyrus	Right	36	-56	36	4.81	1
Cuneus	Right	18	-66	36	4.81	2

9 PUBLICATIONS

Arikan, B.E., van Kemenade, B.M., Podranski, K., Steinsträter, O., Straube, B., Kircher, T. (manuscript submitted for publication).

Arikan, B.E., van Kemenade, B.M., Harris, L.R., Straube, B., Kircher, T. (2017). Voluntary and involuntary movements widen the window of subjective simultaneity. *Iperception 8(4)*, doi:10.1177/2041669517719297.

van Kemenade, B.M., **Arikan, B.E.,** Kircher, T., Straube, B.(2017). The angular gyrus is a supramodal comparator area in action–outcome monitoring. Brain Struct Func., 1-13, 28439662, doi:10.1007/s00429-017-1428-9.

Straube, B., van Kemenade, B.M., **Arikan, B.E.,** Fiehler, K., Leube, D.T., Harris, L.R., Kircher, T. (2017). Predicting the Multisensory Consequences of One’s Own Action: BOLD Suppression in Auditory and Visual Cortices. *PLoS One 12*, e0169131. doi:10.1371/journal.pone.0169131.

van Kemenade, B.M., **Arikan, B.E.,** Kircher, T., Straube, B. (2016). Predicting the sensory consequences of one’s own action: First evidence for multisensory facilitation, *Atten Percept Psychophys.,*1-12. doi:10.3758/s13414-016-1189-1.

Buyukturkoglu, K., Roettgers, H., Sommer, J., Rana, M., Dietzsch, L., **Arikan, B. E.,** Veit, R., Malekshahi, R., Kircher, T., Birbaumer, N., Sitaram, R., Ruiz, S. (2015). Self-Regulation of Anterior Insula with Real-Time fMRI and Its Behavioral Effects in Obsessive-Compulsive Disorder: A Feasibility Study. *PLOS One, 10(8)*, e0135872. doi: 10.1371/journal.pone.0135872.

10 CURRICULUM VITAE

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11 VERZEICHNIS DER AKADEMISCHEN LEHRER

Meine akademischen Lehrer waren die Damen/Herren in Marburg:

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van der Stigchel

In Nijmegen, Niederlande:

Medendorp

Toni

In Leiden, Niederlande:

Hommel

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13 EHRENWÖRTLICHE ERKLÄRUNG

Ich erkläre ehrenwörtlich, dass ich die dem Fachbereich Medizin Marburg zur Promotionsprüfung eingereichte Arbeit mit dem Titel ‘Behavioral and neural indices of perceiving multisensory action outcomes’ in der Klinik für Psychiatrie und Psychotherapie unter Leitung von Prof. Dr. Tilo Kircher mit Unterstützung durch Prof. Laurence Harris und Prof. Katja Fiehler ohne sonstige Hilfe selbst durchgeführt und bei der Abfassung der Arbeit keine anderen als die in der Dissertation aufgeführten benutzt habe. Ich habe bisher an keinem in- oder ausländischen Medizinischen Fachbereich ein Gesuch um Zulassung zur Promotion eingereicht, noch die vorliegende oder eine andere Arbeit als Dissertation vorgelegt.

Ich versichere, dass ich sämtliche wörtlichen oder sinngemäßen Übernahmen und Zitate kenntlich gemacht habe.

Mit dem Einsatz von Software zur Erkennung von Plagiaten bin ich einverstanden.

Vorliegende Arbeit wurden (oder werden) in folgenden internationalen Fachzeitschriften veröffentlicht:

Arikan, B.E., van Kemenade, B.M., Podranski, K., Steinsträter, O., Straube, B., Kircher, T. (manuscript submitted for publication).

Arikan, B.E., van Kemenade, B.M., Harris, L.R., Straube, B., Kircher, T. (2017). Voluntary and involuntary movements widen the window of subjective simultaneity. *Iperception 8(4)*, doi:10.1177/2041669517719297.

Straube, B., van Kemenade, B.M., **Arikan, B.E.,** Fiehler, K., Leube, D.T., Harris, L.R., Kircher, T. (2017). Predicting the Multisensory Consequences of One’s Own Action: BOLD Suppression in Auditory and Visual Cortices. *PLoS One 12*, e0169131. doi:10.1371/journal.pone.0169131.

Ort, Datum, Unterschrift

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Die Hinweise zur Erkennung von Plagiaten habe ich zur Kenntnis genommen.

Ort, Datum, Unterschrift Betreuer

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