THE NEURAL CORRELATES OF AUTOMATIC IMITATION

BY

VICTORIA SCHROEDER

A thesis submitted to the University of Birmingham for the degree of

DOCTOR OF PHILOSOPHY

College of Life and Environmental Sciences

School of Sport, Exercise and Rehabilitation Sciences

University of Birmingham

September 2018

Abstract

The studies in this thesis examine whether humans have developed a specialized neural network to process biological stimuli. It is known that humans imitate and that such non-verbal behaviour is important for social well-being. However, since decades it has been an endeavour to answer the question whether imitation is an innate behaviour, which has evolved through natural selection or whether imitation is learned by experience throughout the lifespan. The present thesis includes four behavioural and two imaging studies, which are aimed at answering this question. This is done by comparing the automatic tendency to imitate (biological stimulus-response mappings) with non-biological stimulus-response mappings. The behavioural studies revealed very similar effects for biological and non-biological stimuli. In both cases, the responses were depending in the experimental tasks, which suggested that spatial and biological stimuli were processed alike. However, the imaging studies revealed different neural networks for the processing of biological and spatial cues. Whereas, the former evoked activity in mirror neuron areas, the latter elicited activity in areas associated with cognitive and response control. The studies therefore suggest that biological and non-biological S-R mappings do affect behaviour similarly but that the underlying neural networks differ.

Acknowledgements

Firstly, I would like to thank my supervisors Dr Craig McAllister and Prof Klaus Kessler for the last four years of incredible support and encouragement. It has been very nice working with you and I appreciate your efforts very much. Further, I would like to thank my fellow PhD students at the University of Birmingham and Aston University for the great and inspiring time spend together. I wish to thank my family (Ulrich, Ursula, Anna and Lise) and my fiancé (Fatjon) for all the times that they put a smile on my face although the work was quite hard. Lastly, I want thank all the people participating in the experiment. Without you it would simply not have been possible to finish any work.

Contents

List of Tables

List of Figures

0 Acronyms

0.0.1 Abbreviations

Acronym	Explanations
-	-
Congruency	**Effects**
BCy	Biological Congruency
SCy	Spatial Congruency
-	-
S-R	**Tasks**
S-R	Stimulus Response
sS-R	Spatial Stimulus Response
bS-R	Biological Stimulus Response
OS-R	Opposite Stimulus Response
sOS-R	Spatial Opposite Stimulus Response
bOS-R	Biological Opposite Stimulus Response
-	-
Imaging	**Techniques**
BOLD	Blood-oxygen-level dependent imaging
EEG	Electroencephalography
FMRI	Functional magnetic resonance imaging
LRP	lateralized readiness potential
MEG	Magnetoencephalography
TFR	Time frequency representation
PET	Positron emis- sion tomography
SPECT	Single photon emission computed tomography
-	-
Other	**Abbreviations**
ASD	autistic spectrum disorder
MN(s)	Mirror neuron(s)
RT(s)	Reaction Time(s)

Table 1: Abbreviations used in the thesis

0.0.2 Acronyms - brain areas

Acronym	Explanation
AG	Angular gyrus
FEF	Frontal eye fields
FG	Fusiform gyris
FPC	Frontopolar cortex
FrO	Frontal operculum
GR	gyrus rectus
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
LG	Lingual gyrus
MFG	Medial frontal gyrus
PaO	Parietal operculum
PFC	Prefrontal cortex
PO	Pars opercularis
PPC	Posterior parietal cortex
S1	Primary sensory cortex
SMA	Supplementary motor area
SMG	Supramarginal gyrus
SPL	Superior parietal lobule
SPC	Superior Parietal Cortex
STC	Superior temporal cortex
STS	Superior temporal sulcus
TPJ	Temporal parietal junction
V1	Primary visual cortex
VAA	Visual association area

Table 2: Acronyms for brain areas used in the thesis

0.0.3 Acronyms - muscles

Acronym	Explanation
FDI	First dorsal interosseous
FDS	Flexor digitorum superficialis
OP	Opponents pollicis

Table 3: Acronyms for muscles used in the thesis

1 Chapter 1

1.1 General introduction

Humans communicate using words and gestures, and for a long time, it has been a great endeavour to understand why humans have developed non-verbal communication and what function it has. A particular form of non-verbal communication is imitation – the process during which observed movements or expressions are repeated by the observer. This occurs in all social situations and without awareness of the people involved (Heyes, 2011). Already in the 18th-century imitation in social settings was understood as a form of sympathy (Smith, 1976). However, imitation and its effects were not assessed experimentally until the 20th century.

Miller and Dollard (1941) assessed imitation in the context of social learning. Here it was proposed that people learn through imitation if the observer has a motivation to do so by positive reinforcement. Bandura (1962) expanded on the social learning theory, stating that imitation occurs if imitating supports the individual's goal. Although reinforcement or punishment affects the learning rate, imitation also happens by the mere observation of behaviour, without any immediate learning goal. Wheeler and Caggiula (1966) termed this 'behavioural contagion'. For example, participants observing aggressive in contrast to gentle behaviour, displayed more aggressive actions themselves.

These early studies emphasized the social context during imitation. Imitation increased if the observer liked the actor (van Baaren, Holland, Kawakami, & van Knippenberg, 2004) resulting in more kind behaviour (e.g. giving larger tips to a waiter; (van Baaren, Holland, Steenaert, & van Knippenberg, 2003). Today, it is known that imitation in social settings (motor mimicry) is unconscious and closely linked to social well-being between peers (Chartrand & Van Baaren, 2009). Motor mimicry is usually studied by assessing the frequency of imitation within a predefined time window (van Baaren et al., 2003). It has been observed repeatedly for mannerism (Chartrand & Bargh, 1999), postures (Chartrand & Van Baaren, 2009), facial expressions (Chartrand & Bargh, 1999), and speech patterns (Bock, 1986). Since motor mimicry is observed in a variety of situations and is beneficial for social interactions (Stel, van Dijk, & van Baaren, 2016; Y. Wang & Hamilton, 2012), it has been suggested that humans have developed such behaviour

to promote social well-being (Stel & Vonk, 2010). However, this rather bold hypothesis needed to be tested more rigorously, and therefore, it has become a great endeavour to gain more insights into the cognitive processes leading up to imitation.

Automatic imitation is motor mimicry measured in a controlled laboratory setting and it occurs when participants imitate unconsciously and automatically although the task does not require it. Further, imitation occurs when it is beneficial for responding or when it interferes with responding (Heyes, 2011). In contrast to motor mimicry, automatic imitation is measured in a computer-based paradigm, in which the participants observe biological and non-biological stimuli on a monitor. Heyes (2011) suggested that automatic imitation draws on similar cognitive mechanisms as conscious imitation. But, whereas conscious imitation incorporates additional cognitive mechanisms related to working memory, automatic imitation does not (Catmur, Walsh, & Heyes, 2009; Bien, Roebroeck, Goebel, & Sack, 2009). Therefore, it has been recommended to study automatic imitation to understand the mechanisms underlying the copying of human actions.

1.1.1 Automatic imitation, behavioural paradigms and general findings.

Automatic imitation has been studied using three different paradigms: A simple response paradigm, a stimulus-response (S-R) paradigm and a simple-response kinematic-movement paradigm.

In the simple-response paradigm, a biological stimulus (e.g. a hand) is presented on the screen. This stimulus performs different movements. Depending on the experimental block participants are told to execute a specific movement with the hand as well. Therefore, they perform the same response regardless of the shown stimulus on each trial of the same block. On some trials, the executed movement directory and the used effector (e.g. finger, hand, foot) are similar to the movement directory and the identity of the stimulus on the screen (compatible), whereas they are different on other trials (incompatible). Participants react faster and make fewer errors on compatible in comparison to incompatible trials (Press, Bird, Flach, & Heyes, 2005). [1]

S-R paradigms are very similar to simple-response paradigms. However, instead of using

[1]Compatible is used when the imperative (task-relevant) stimulus creates the match or mismatch between the observed and executed behaviour

block-dependent responses, participants make different responses based on an imperative stimulus on the screen. A pioneering experiment, (Brass, Bekkering, Wohlschläger, & Prinz, 2000) presented a hand moving the index or the middle finger on the screen, which was not relevant to the task (task-irrelevant stimulus). Also, a number (e.g. "1" or "2") was shown, which prompted the participants to move their index or middle finger. Depending on the trial, responses could be similar (biologically congruent) or dissimilar (biologically incongruent) to the finger movement on the screen (task-irrelevant stimulus). On biologically-congruent trials, participants responded faster and made fewer errors than on biologically-incongruent trials. It is important to note that all S-R paradigms have a task-relevant stimulus (imperative stimulus), which prompt a specific response based on its features. Additionally, the experiment must have a task-irrelevant stimulus, which manipulates the match/mismatch between observed and executed actions. [2].

The simple-response kinematic-movement paradigm is also very similar to the simple-response paradigm. However, instead of measuring reaction times (RTs) deviations in the movement trajectory are investigated. For example, participants are asked to perform simple movements with their hand/arm while observing an experimenter performing similar movements. Depending on the trial, the movement of the experimenter and the participant is similar (compatible) or dissimilar (incompatible). On incompatible trials, the participant exhibits more movement irregularities in the movement trajectory (Kilner, Paulignan, & Blakemore, 2003). All these experiments have revealed that participants perform better when the observed actions match the executed actions. On the other hand, seeing different actions interferes with the executed response.

1.1.2 Theories of automatic imitation and similarities with spatial cueing

The ideomotor theory provides the most accepted explanation for why automatic imitation occurs. The ideomotor theory had its origin in the United Kingdom, and Germany and these slightly differing accounts were summarized by James (James, 1890; Stock & Stock, 2004) in his book Principles of Psychology. The ideomotor theory was based on the simple principle that humans initiate actions because of their future sensory consequences.

[2]If the task-irrelevant stimulus creates the match/mismatch between observed and executed actions the words congruent/incongruent are used.

To know which actions elicit which consequences these relationships need to be learned through repeated coupling of action execution and action consequence (associative learning). Once these bidirectional relationships have been formed, an action is automatically executed whenever its consequence has been mentalized. Accordingly, automatic imitation occurs because an observed action triggers the mentalization of action-consequences, which results in an imitated action. When a person needs to go against this automatic behaviour, action inhibition is required, which increases RTs and behavioural errors.

The common coding theory is an extension of the ideomotor theory and explains in more detail how the perceived sensory information can trigger actions (Aschersleben & Prinz, 1995). Accordingly, sensory information can trigger the mentalization of action goals by sharing features with these goals. For example, when observing another person sitting cross-legged, an action-consequence (sitting cross-legged) will trigger the corresponding action, despite seeing another person. This tendency becomes stronger the more the similarity between actor and observer increases. Importantly, the ideomotor theory and the theory of common coding not only applies to biological stimuli (e.g. actions or displayed facial emotions) but also to non-biological stimuli (e.g. changes in colour or spatial dimensions). For example, when observing a grasp towards an object placed in the observer's right hemifield, the spatial position (right hemifield) will prompt an action to the right side and interfere with an action to the left side.

The dimensional overlap model by Kornblum, Hasbroucq and Osman (1990) pointed out why the interference effects occur. The model is based on the common coding theory but in addition it suggests that observed stimuli elicit behaviour based on input from two distinct cognitive pathways. The task-irrelevant information is processed quickly in a direct and automatic route, which always activates the response matching the stimulus. The imperative stimulus is processed in a deliberate route, which takes external factors (e.g. task instructions) into account. If the information of the automatic and deliberate routes correspond (congruent trials), a response is activated quickly. However, if the output from the automatic and the deliberate routes do not correspond (incongruent trials), the S-R mapping rule defined by the task instructions needs to be applied, which increases RTs. Barber and O'Leary (1997) proposed that the automatic and deliberate pathways described in the dimensional-overlap model could be distinguished in the form

of short-and long-term S-R associations. Accordingly, the deliberate route uses short-term S-R associations, which are arbitrarily based on the task instructions. These rules are only relevant at the specific moment but can influence behaviour in subsequent tasks, as well (Tagliabue, Zorzi, Umiltà, & Bassignani, 2000). In contrast, the automatic processes are activated based on learned, long-term S-R associations. These are unaffected by task instructions and based on experience (Umiltà & Zorzi, 1997).

In conclusion, automatic imitation can be explained by generic S-R mapping processes, which also explain spatial S-R mappings. Many studies have compared behavioural effects elicited by spatial and biological stimuli to assess whether the stimuli types, despite similar theoretical backgrounds, trigger different behavioural effects, which could support the idea that humans have developed a unique cognitive circuit to process biological stimuli (Rizzolatti & Craighero, 2004). Before illustrating these experiments, the spatial equivalent to automatic imitation will be demonstrated in more detail.

1.1.3 Spatial congruency effects

The spatial equivalent to automatic imitation has been called spatial congruency (SCy) effect or Simon effect (Simon, 1969). For simplicity, automatic imitation will also be referred to as biological congruency (BCy) effect in the course of this thesis. The original study examining the SCy effect (Simon 1969) used auditory stimuli in an S-R task. Participants heard the words 'left' or 'right' in the left or right ear. When the word left was heard, participants pressed a response key located on the left side and vice versa. It was of interest whether responses were affected by the side of the auditory input. Indeed, RTs were faster if the side (left vs. right) of the auditory input corresponded to the side (left vs. right) of the button press. Simon and Craft (1970) replicated these results with visual stimuli. They presented colour stimuli on the right or left side of the screen and prompted participants to respond by pressing a button that matched the presented colour. The buttons were located to the left and right side of the participant. Responses were faster if a right-side button press followed a stimulus located on the right side. The results of both studies showed that spatial information that was task-irrelevant influenced performance. In other words, when the task-irrelevant stimulus was spatially-congruent with the response, they facilitated the response, whereas an interference effect was observed when

the task-irrelevant stimulus and the response were spatially-incongruent. These results were first taken as evidence that humans have a "natural tendency to respond towards the [spatial] source of stimulation". This effect has now been replicated in a wide variety of experiments using auditory (Mewaldt, Connelly, & Simon, 1980; Simon & Acosta, 1982; Simon, Craft, & Webster, 1973), horizontally and vertically displayed visual stimuli (Nicoletti & Umilta, 1985) and object characteristics (Tucker & Ellis, 1998). All experiments show faster and more correct responses when the stimulus and the response are spatially-congruent in comparison to spatially-incongruent. However, in general, auditory Simon effects are larger than the visual equivalent (Vu, Proctor, & Urcuioli, 2003) and the size of the visual effect depends on stimulus discriminability (Hommel, 1993; Proctor & Lu, 1994).

1.1.4 Are spatial and biological stimuli processed similarly?

From these findings and the findings of automatic imitation, it can be concluded that spatial and biological stimuli show facilitation effects when the stimuli have similar features as the executed response and interference effects when the stimuli and response are dissimilar. Since the early 21st century, studies have compared BCy and SCy effects. Brass et al. (2000) presented a right hand on the screen, which could perform a lifting movement with the index or middle finger. A cross was superimposed on the nail of the moving or stationary finger. In the spatial task, participants identified the finger with the superimposed cross and performed a lifting movement with the same finger. Simultaneously, the hand could either perform a lifting movement with the identical finger (biologically-congruent) or not (biologically-incongruent). In the biological task, the participants reacted with the same finger, which performed the lifting movement on the screen. Simultaneously, the cross was either on that finger (spatially-congruent) or on the static finger (spatially-incongruent). Both tasks revealed a congruency effect, which means that RTs were faster in the biologically-congruent/spatially-congruent conditions than in the biologically-incongruent/spatially-incongruent conditions respectively. However, since the magnitude of the BCy effect was larger than the magnitude of the SCy effect, it was concluded that biological stimuli trigger stronger facilitation effects during congruent trials and stronger interference effects during incongruent trials. Accordingly,

biological stimuli are processed more automatically than spatial stimuli. Whereas it is widely accepted that biological and spatial stimuli elicit congruency effects, many studies have revealed no differences in SCy and BCy effects (Jansson, Wilson, Williams, & Mon-Williams, 2007; Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff, 2010). Therefore, the differences in effect size between SCy and BCy effects reported in other studies could be due to differences in stimulus saliency [3] and not due to the biological and spatial features of the task-irrelevant stimuli (Jansson et al., 2007). Further, it has been argued that many studies have used task-irrelevant biological stimuli, which incorporated spatial features since they were presented in the left or the right hemifield (Brass et al., 2000; Brass, Bekkering, & Prinz, 2001). Hence, the BCy effects would partly be triggered by the spatial characteristics of the task-irrelevant stimulus.

Based on the insights from BCy and SCy effects triggered in the experiment of Brass (2000), Sauser and Billard (2006) proposed two distinct computational models predicting the cognitive processes when spatial and biological stimuli are processed alike or differently. The single-route model is based on the assumption that spatial and biological cues are processed along the same route (Figure 1). After the perception of the spatial and biological cues in the superior temporal sulcus (STS) and medial superior temporal cortex (STC), both stimuli are updated to fit S-R mappings in the posterior parietal cortex (PPC) before the response is selected in the ventral premotor cortex (vPMC) and subsequently executed. Importantly, the prefrontal cortex (PFC) influences the S-R mapping by integrating response rules defined by the task instructions. In contrast, the direct-matching model includes a distinct pathway for biological and spatial cues (Figure 2) . Whereas spatial cues are processed in the same pathway as in the single-route model, biological cues bypass S-R mappings in the PPC, which is influenced by the PFC and the task instructions. Instead, biological cues influence behaviour by directly mapping the observed behaviour onto the observer's motor system within the vPMC. Both the single-route and direct-matching model predict SCy and BCy effects in S-R tasks. Therefore, it is impossible to distinguish the neural circuits evoking SCy and BCy effects using such tasks. Sauser and Billard (2006) proposed a solution, which drew on the work of Hedges and Marsh (1975), who introduced the opposite stimulus-response (OS-R) paradigm.

[3] How easy the spatial or biological stimuli can be identified

Single-Route Model from Sauser and Billard (2006)

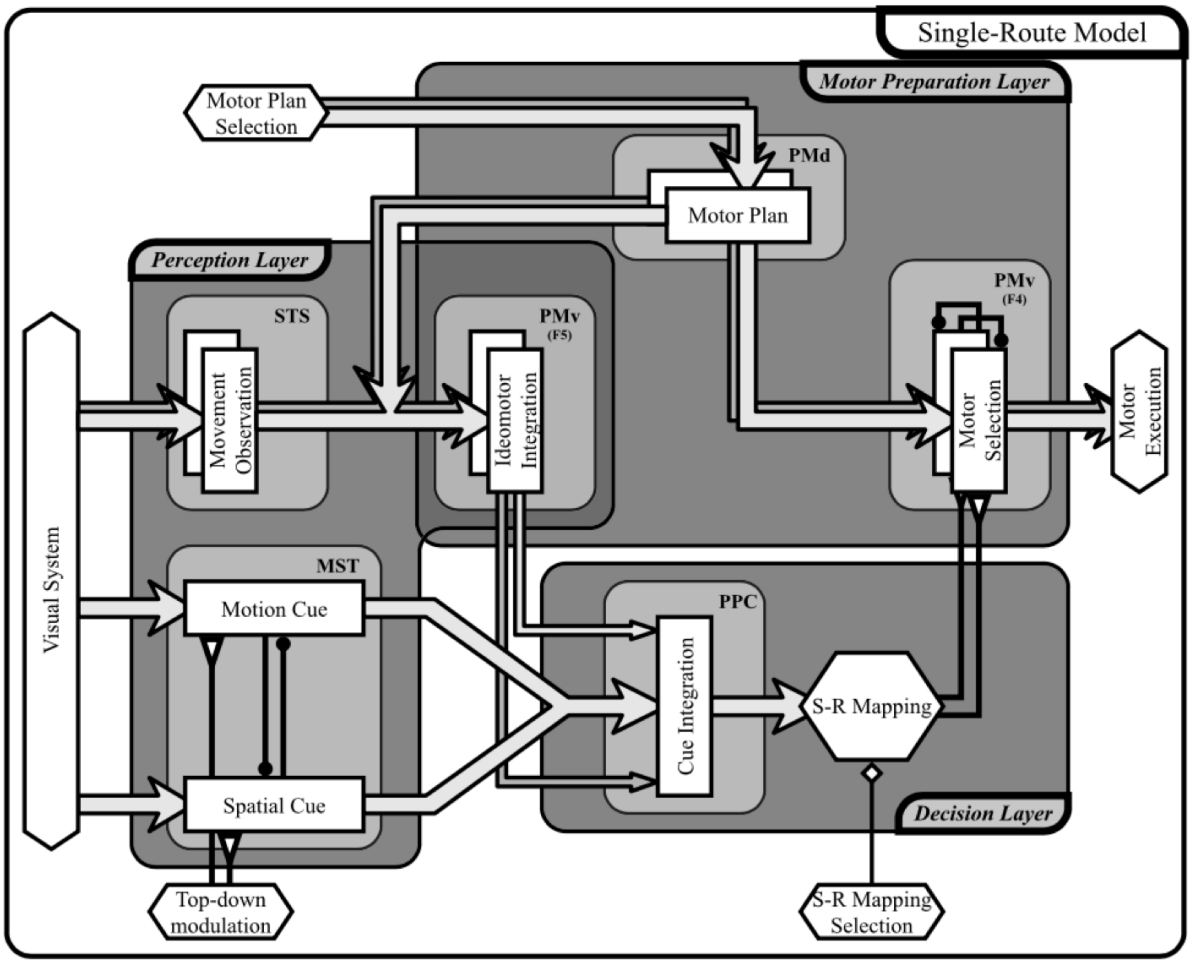


Figure 1: Shows the single-route model from Sauser and Billard (2006) directly copied from the respecting paper. It shows that task-irrelevant biological and spatial stimuli are processed in similar cognitive routes. For both stimulus types the stimulus-response mappings are processed in the posterior parietal cortex. The prefrontal cortex processes the mapping rules from the task instructions and incorporates these into the stimulus-response mapping of the task-irrelevant stimuli. Therefore, the congruency effects in the S-R tasks are flipped to a reversed congruency effect in the OS-R tasks for both stimulus types. See, A Figure 31 for the legend explaining the different arrows seen in the Figure.

Direct-Matching Model from Sauser and Billard (2006)

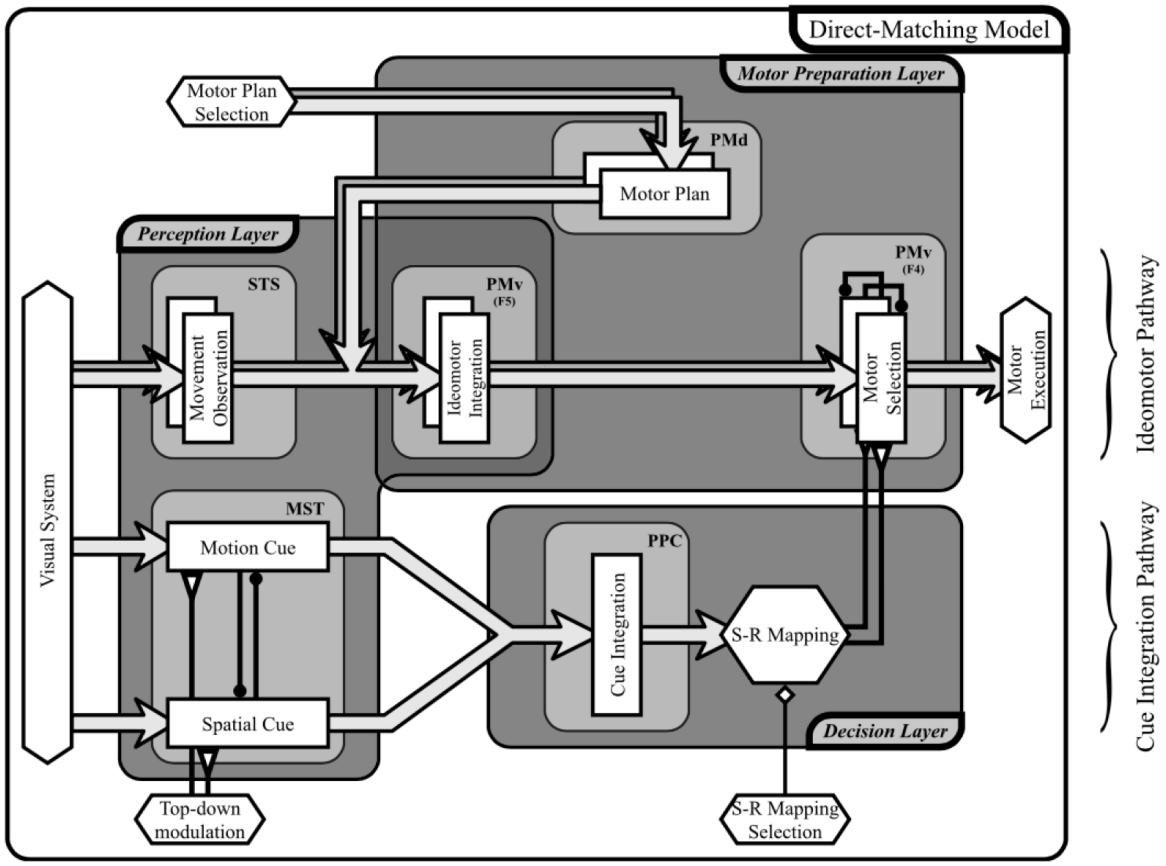


Figure 2: Shows the direct-matching model from Sauser and Billard (2006) directly copied from the respecting paper. It shows that task-irrelevant biological stimuli are processed in a direct observation-execution matching route in the ventral premotor cortex. Spatial task-irrelevant stimuli are processed in the same route as in the single-route model. See, A Figure 31 for the legend explaining the different arrows seen in the Figure.

The experimental stimuli of the OS-R task were identical to the S-R task explained in the section 'Spatial congruency effects' (Craft & Simon, 1970), but Hedge and Marsh (1975) instructed the participants to press the response key with the colour that did not match the imperative stimulus. Here, the results showed a reversed spatial congruency (R-SCy) effect such that RTs were faster if the imperative stimulus was presented on the opposite side as the required response (spatially-incongruent) than when it was presented on the same side (spatially-congruent). The R-SCy effect was explained by logical recoding, a mechanism by which the task instructions, which determine the correct S-R mapping applied to the imperative stimulus, also affect the S-R mapping applied to the task-irrelevant stimulus. If the response rule prompts participants to react with a matching response to the imperative stimulus, the matching (congruent) response is faster for the task-irrelevant stimulus as well. However, if the response rule prompts participants to react in a non-matching manner to the imperative stimulus, then the non-matching (incongruent) response to the task-irrelevant stimulus is faster.

The single-route and direct-matching models from Sauser and Billard (2006) propose different results for task-irrelevant spatial and biological stimuli in the OS-R task. The single-route model predicts a R-SCy as well as a reversed biological congruency (R-BCy) effect for both types of task-irrelevant stimuli respectively. The direct-matching model predicts a R-SCy effect but no R-BCy effect. A recent study aimed at testing the predictions of the single-route and direct-matching models and set-up experiments to trigger SCy/BCy and R-SCy/R-BCy effects in S-R and OS-R tasks (Boyer, Longo, & Bertenthal, 2012). Whereas both stimuli triggered congruency (SCy/BCy) effects in the S-R tasks, only a R-SCy effect was found in the OS-R task. Therefore, the behavioural results supported the direct-matching model (Boyer et al., 2012).

All in all, behavioural studies reveal BCy and SCy effects. These effects from biological and spatial stimuli could be based on the same cognitive mechanisms explained by the ideomotor theory. However, evidence exists, which shows that task-irrelevant spatial cues are processed differently depending on the task instructions, whereas the processing of task-irrelevant biological cues is not affected similarly.

Behavioural findings can only show indirect evidence for potential neural mechanisms. Therefore, imaging studies are required to address the behavioural findings and provide

direct evidence about the neural pattern observed during SCy/BCy and R-SCy/R-BCy effects. The investigation of the neural activity during automatic imitation can focus on different aspects. For example, the neural underpinnings of the behavioural facilitation during biologically and spatially congruent trials can be compared. Secondly, the inhibition of automatic imitation and automatic spatial cueing during incongruent trials can be assessed. Lastly, the logical recoding for spatial stimuli in the OS-R task could be examined and compared to the neural pattern for biological cues in a similar task. Surprisingly, very little imaging work has been done on the neural underpinning during automatic imitation and most of such insights come from mirror neuron studies.

1.1.5 Mirror neurons and automatic imitation

Automatic imitation could rely on mirror neuron (MN) activity (Bien et al., 2009; Brass, Derrfuss, & Von Cramon, 2005; Catmur et al., 2009; Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2011; Simpson, Murray, Paukner, & Ferrari, 2014). In 1992 MNs were coincidentally found in macaque monkeys by the use of single cell recordings. In this study, monkeys were required to manipulate objects while neurons in the area F5 were recorded. By accident, it was observed that the same neurons, which fired during the execution of the movements also fired when the monkey observed the experimenter perform similar movements (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). In a follow-up study neurons in the monkey's F5 were systematically recorded while the monkey executed different movements and saw the experimenter execute the same, similar or distinct movements (Gallese, 1996). This revealed three different classes of MNs: Strictly congruent MNs, which fired when the same movement was executed and observed; Broadly congruent MNs, which fired when a similar movement was executed and observed, and Non-congruent MNs, which did not show any meaningful link between the observed and executed actions but fired whenever an action was observed and executed. It was suggested that during the observation of actions MNs are activated to internally replay the observed action and thereby the observer can understand the purpose of the observed action. This could further be important for observational learning and when choosing an appropriate response to an observed action (Gallese, 1996). To date a wide variety of functions have been attributed to the MN system. Accordingly, they are essential for processing

intransitive movements (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003), actions in different areas of intrapersonal space (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009), actions from different viewing perspectives (Cisek & Kalaska, 2004), action-reward contingencies (Caggiano et al., 2012), and actions with differing movement velocities (Tkach, Reimer, & Hatsopoulos, 2007).

The only single cell study in humans was done 18 years after the discovery of MNs (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Cells from 21 patients were recorded while they read the words 'Hand' or 'Finger' and subsequently reached for a cup. They also saw movies showing the same movement. During control trials, the words 'Hand' or 'Finger' were displayed, but the participants kept still. A second experiment followed the same structure but involved the words 'smile' or 'frown' and the corresponding facial expressions. The parahippocampal gyrus had more MNs responding to grasping movements whereas the dorsal anterior cingulate cortex (ACC) contained more MNs responding to facial expressions. In general, the hippocampus, parahippocampal gyrus, entorhinal cortex and supplementary motor area (SMA) were equipped with a significant amount of strictly congruent MNs. These results showed that humans likely have a MN system as well, which could map perceived actions onto the observer's motor system.

1.1.6 Functional magnetic resonance imaging studies assessing MN activity

Many functional magnetic resonance imaging (fMRI) studies have also assessed the neural correlates of the human MN system by examining which areas are active when a person observes and executes actions. A review (Molenberghs, Cunnington, & Mattingley, 2012) compared 125 of these studies and found that core MNs areas in macaque monkeys such as the inferior parietal lobule (IFL), the inferior frontal gyrus (IFG) and the vPMC also exhibit mirroring properties in humans. However, areas unrelated to the monkey's MN system, such as the primary visual cortex (V1) or the limbic system revealed MN properties in humans as well. fMRI studies have also used adaption paradigms to assess MN activity. These studies work on the premise that neurons habituate to repeated exposure of the same input and therefore become less active over time. The fMRI blood-oxygen-

level dependent (BOLD) [4] response also decreases when a person has been exposed to the same stimuli repeatedly. fMRI adaption studies have shown that the IFG, a core MN area, decreases in BOLD response if an executed action is proceeded by a similar rather than dissimilar observed action and vice versa (Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Press, Catmur, et al., 2012). Hence, the same neurons in the IFG are likely processing executed and observed actions. However, other studies have not been able to replicate these findings (Dinstein, Hasson, Rubin, & Heeger, 2007; Lingnau, Gesierich, & Caramazza, 2009).

Importantly, all action execution-observation paradigms share one critical limitation: the paradigm only shows that areas might be active during execution and observation of actions, but this might have no implications for behaviour. Since modern neuroscience has rejected phrenology, it is likely that brain areas are activated by different tasks (e.g. observation and execution of actions). Therefore, it is essential to include a behavioural measure to assess which consequences MN activation has on behaviour.

One endeavour has been to assess the neural correlates of automatic imitation in an S-R or simple-response paradigm using fMRI, but only a few studies have done so (Brass et al., 2001, 2005; Bien et al., 2009; Mengotti, Corradi-Dell'Acqua, & Rumiati, 2012; Cross, Torrisi, Reynolds Losin, & Iacoboni, 2013). However, the studies which compared the neural activation leading up to BCy and SCy effects (or the comparable compatiblity effects) have found evidence that biological stimuli uniquely activate areas with MNs properties (IFG, right PMC, middle frontal gyrus (MFG), parietal operculum located in the IPL, precuneus, angular gyrus (AG) and temporoparietal junction (TPJ). Unfortunately, many of these imaging studies incorporated the same limitations as the behavioural studies. First, biological task-irrelevant stimuli incorporated spatial features (e.g. a biological movement appearing in the left or the right hemifield), which means that the results of automatic imitation could not be attributed to the biological stimulus per se (Brass et al., 2001, 2005; Bien et al., 2009; Cross et al., 2013). Secondly, the neural correlates of automatic imitation have not been compared with an appropriate control condition. For example, Brass et al. (2001) did not use a control condition at all, and Brass et al. (2005)

[4] fMRI BOLD response is the measure of blood-oxygen-levels in the brain and therefore an indicator where the most energy is being used in the brain

compared the neural activation during automatic imitation with the neural correlates activated by an entirely different experimental task, which differed in a variety of features aside from the biological/non-biological nature of the presented stimulus. Lastly, fMRI studies assessing differences between biological cueing and spatial cueing average the signal over multiple seconds. Since RTs during automatic imitation are in the milliseconds' range, the results from fMRI studies do not indicate whether the differences in neural activity are related to response preparation or post-response mechanisms.

1.1.7 Insights from transcranial magnetic stimulation

Evidence from transcranial magnetic stimulation (TMS) studies can solve some of these limitations. With TMS it is possible to apply local current stimulation over a part of the human cortex, which can either disrupt or trigger the neural activity of the underlying areas. When applying a single current pulse to the primary motor cortex (M1), it is possible to evoke a muscle contraction (motor evoked potential, MEP) in the limb corresponding to the stimulated brain area. In one such experiment (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), participants observed different movements or objects while MEPs were elicited. In the grasp condition, participants observed an experimenter grasping towards one of several different objects. In the object condition, the participants only observed an object. In the arm condition, the participants observed the experimenter drawing a large geometrical shape in the air with his whole arm and hand. In the last condition, the participants had to detect when a light was dimming by verbally responding. MEPs were evoked by stimulating the participants' M1 during each of the conditions. Activity from different muscles was measured (flexor digitorum superficialis (FDS), first dorsal interosseous (FDI) and opponents pollicis (OP)). The results revealed that the observation of an action selectively activated the muscles used in the observed action (Fadiga et al., 1995; Catmur, Walsh, & Heyes, 2007; Enticott, Rinehart, Tonge, Bradshaw, & Fitzgerald, 2010). This shows that action observation indeed lowers the threshold for imitation. The problem here lies in the location of TMS. All MEP studies stimulated the M1. Although the M1 also contains MNs (Vigneswaran, Philipp, Lemon, & Kraskov, 2013), the core of the MN network includes the IFG, vPMC and the IPL, and the TMS studies do not show whether MN activity in these areas is necessary for the observed effects.

Therefore, additional TMS studies have stimulated these areas to investigate the causal link between the MN system and action perception. For example, MEPs decrease after viewing finger movements, if (disrupting) mirror neurons areas such as the vPMC and S1 have been stimulated (disrupted). On the other hand, repetitive TMS outside of these mirror neurons areas do not influence mirroring (Avenanti, Bolognini, Maravita, & Aglioti, 2007). Pobric and Hamilton, (2006) and Tidoni et al. (2013) made participants judge the effort of perceived actions (lifting a heavy or light box). Repetitive TMS to the IFG and not to control regions increased erroneous responses. Important, such performance worsening by IFG stimulation was only present for observed motor actions and not for temporal or spatial control conditions. These results are in line with studies showing that the ability to discern slightly different movements is impaired by IFG stimulation (Jacquet & Avenanti, 2013; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007; Urgesi, Candidi, Ionta, & Aglioti, 2007). Hence, the IFG is important when understanding perceived actions.

Further, single TMS pulses to the IFG time-locked to a target stimuli reverses movement priming effects. Without TMS participants are faster when judging the velocity of an observed movement, if this stimulus is preceded by a congruent prime. Single-pulse TMS to the IFG reverses this effect so that participants react faster to counter-primed stimuli (Cattaneo, 2010). Lastly, motor - to visual adaption [5] is disrupted by biphasic TMS to the IFG, which stresses that the IFG not only is involved in perceiving actions but also in the integration of executed and perceived actions (e.g. in mirroring) (Cattaneo et al., 2010).

TMS has also been used to gain more insights into the timing of mirror neuron responses. For example, Cavallo et al. (2013) used a single-pulse TMS paradigm to assess motor cortex activation after observed actions. They concluded that motor mirroring was present 200 ms after the observed action onset. However, Ubaldi et al. (2013) have suggested that the PPC modulates mirroring responses earlier than 200 ms after stimulus onset, whereas frontal areas are more involved later on. That mirroring processes are divided into two separate stages was also shown by Barshiesi et al. (2012). They induced fast wrist mirroring movements by TMS to the M1 and observed that counter mirror training

[5]The effects by which the repetition of a specific executed movement facilitates the categorization of a counter-movement

[6] only influenced the induced movements, if stimulation happened 320 ms after stimulus onset.

Especially important for this line of work, are TMS studies, which stimulate mirror neurons areas while participants engage in automatic imitation and the spatial equivalent. Here it has been shown that stimulation to the IFG or intra parietal lobule (IPL) decreases automatic imitation, which is likely due to decreases in RTs during the biologically-incongruent in comparison to the biologically-congruent condition. In contrast, TMS to the IFG or IPL does not affect SCy effects (Catmur et al., 2009; Mengotti, Ticini, Waszak, Schütz-Bosbach, & Rumiati, 2013). Hence, it can be concluded that the IFG likely contributes to BCy effects but not to SCy effects (these experiments will be described in more detail in chapter 5).

These studies highlight the value of TMS when assessing mirroring mechanisms. However, it is problematic that TMS has a low spatial resolution. That is, TMS does not only affect the area beneath the coil but has wide-ranging neurological effects. Therefore, it is not possible to know whether the behavioural effects seen in these TMS studies were caused by changes in the 'stimulated' area or in the surrounding areas (Walsh & Cowey, 2000).

So far, no study has used Magnetoencephalography (MEG) recordings to examine the neural correlates leading to automatic imitation in an S-R paradigm. This is very surprising since MEG provides methodological advantages that could help to investigate the neural processes leading up to automatic imitation. In order to understand how MEG recordings can contribute to assessing automatic imitation, an introduction to MEG will follow in which the technique will be explained.

1.1.8 An introduction to MEG

MEG, first used by David Cohen in 1968 (Cohen, 1968), provides a non-invasive method for assessing neural activity. MEG measures the magnetic fields created by current flow generated during neuron activation. Unlike other imaging tools (fMRI, positron emission tomography (PET), single photon emission computed tomography (SPECT)), which

[6] The effect by which training to respond with a counter mirror action reduces or reverses the automatic imitation effect (Catmur et al., 2008)

rely on indirect measures of brain activity such as brain metabolism, MEG measures actual neural activity. MEG has high temporal resolution, which enables the assessment of millisecond fluctuations in brain activity. In contrast to electroencephalography (EEG), which records electric current flow from the scalp of the subject and also provides excellent temporal resolution, the MEG system provides the possibility to measure neural activity within the brain (neural sources) when superimposing the MEG recordings with a structural image of the subject's brain. Although this is also possible with EEG measurements, these estimates are less reliable since EEG measures current flow whereas the MEG measures the magnetic field. Whereas the former is disturbed when travelling from its origin to the sensor, non-magnetic materials do not influence the latter. This, in turn, makes MEG source localizations more precise than EEG source reconstructions (Mosher, Leahy, & Lewis, 1999). MEG provides millimetre accuracy when localizing activated sources. With these advantages, MEG provides a great tool to measure fast cognitive processes, relying on discrete brain areas rather than a broadly distributed network (Hari, Levänen, & Raij, 2000).

Of course, MEG also has drawbacks. The neural signal recorded with the MEG is minimal in amplitude. Hence, it is challenging to be picked up by magnetic sensors. Further, the signal is easily distorted by electromagnetic signals in the environment and physiological signals unrelated to the neural activity (e.g. eye blinks or heart rate). Therefore, the recorded data needs to be cleaned before the analysis. Data cleaning has advanced in the recent years, nevertheless, any data cleaning removes actual brain activity along with data artifacts. Hence, the resulting data does not represent the actual activity in the brain. This imposes a third issue, which is known as the inverse problem. In MEG, the magnetic field is measured outside of the head, which is used to gain insights about the activity inside the brain. Since the measurements always include some degree of error and unknown information, the brain activity can only be approximated (Ballet, 2014). Hence, the results of MEG studies always need to be interpreted with some degree of caution.

Broadly speaking, two different analytic procedures can be adopted when analyzing MEG data. First, it is possible to assess event-related fields (ERFs), which are small fluctuations of the whole MEG signal time-locked to an event of interest. ERFs differ

in the magnetic flux density as well as the spatial location [7]. They are very sensitive to temporal manipulations and, hence, provide an excellent analysis when precise temporal insights are required (Woodman, 2010). The present study will focus more on time-frequency signals. Here, the magnetic field measured by the MEG system is converted into a wide-band of electrical signals (from <0.2 Hz to >90 Hz), which can be separated into different frequency bands by means of a Fourier transform, namely infraslow (<0.2 Hz), delta (0.2 to 3.5 Hz), theta (4 to 7.5 Hz), alpha (8 to 13 Hz), beta (14 to 30 Hz), gamma (30 to 90 Hz), and high-frequency oscillations (higher than 90 Hz) (Silva, 2013). The increases/decreases of oscillatory power in these frequency bands in different brain regions have been associated with a variety of cognitive mechanisms. In the present study we will focus on the function of theta, alpha and beta frequencies due to their involvement in mechanisms important for spatial or biological cueing, which will be introduced in the following sections:

1.1.9 The general function of theta activity

To date, theta activity has been related to a variety of cognitive processes. Most commonly, frontal theta has been associated with novelty, error processing and punishment. For example, when observing a deviant stimulus, in the midst of sequentially presented expected stimuli, frontal theta power increases (Cavanagh, Zambrano-Vazquez, & Allen, 2012). Secondly, frontal theta power increases immediately after an error has been executed (Cavanagh, Cohen, & Allen, 2009). Thirdly, medial frontal theta utilizes the occurrence of errors during a reinforcement learning task to slow responses on the next trial (Cavanagh, Frank, Klein, & Allen, 2010).

Essential for the present study, frontal theta has also been related to conflict processing, which will be outlined in more detail in Chapter 4. In general, theta power increases when conflict increases (Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008). For example, the Stroop task [8] triggers enough stimulus-stimulus conflict [9] to elicit frontal theta

[7] In EEG the equivalent to ERFs are event-related potentials (ERPs) and these measure differences in polarity.

[8] In a Stroop task participants see a word naming a colour (e.g. 'red'), which is coloured in a matching or mismatching manner. RTs are longer if semantics and coloring mismatch

[9] Conflict during which the observed stimuli on the screen mismatch and therefore make response selection difficult. This is in contrast to S-R conflict during which an executed response contradicts a learned S-R mapping.

increases (Hanslmayr et al., 2008). Further, the Go/NoGo [10] task elicits frontal theta increases when participants have to withhold a response (Cohen, Van Gaal, Ridderinkhof, & Lamme, 2009). In general, frontal theta increases have been attributed to the allocation of top-down control processes to overcome conflict or to stop a response (Cohen et al., 2012). Although less common in the scientific literature, changes in theta power have also been reported in a variety of other situations: accordingly, theta activity is affected by memory encoding (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010), working memory (Itthipuripat, Wessel, & Aron, 2013) target perception (Urgen, Plank, Ishiguro, Poizner, & Saygin, 2013), selective attention (Green & McDonald, 2008), and anxiety (Suetsugi et al., 2000).

1.1.10 The general function of alpha activity

Alpha is the oscillation centred around 10 Hz (8-12 Hz). The topographies of the detected alpha activity varies with the task demands. Whereas alpha desynchronization in posterior areas is observed during eyes-open in comparison to eyes-closed conditions (Adrian and Matthews, 1934), and when visual spatial attention is required (Händel, Haarmeier, & Jensen, 2011), auditory tasks have evoked alpha desynchronization in a more widespread network involving parietal, prefrontal and temporal areas (Obleser & Weisz, 2012). Although alpha activity has been observed in a variety of different tasks and locations, the underlying function of the oscillation is interpreted similarly. Accordingly, alpha desynchronization in an area is associated with increased activation of the affected brain area. Hence, alpha desynchronization is often related to mental effort and task success: e.g. stronger alpha desynchronization is associated with faster RTs (Lansing, Schwartz, & Lindsley, 1959) and better recall of previously encoded items (Klimesch & W, 1997).

Contrary to the desynchronization of alpha, the synchronization of alpha has been related to reduced information processing (Klimesch, Sauseng, & Hanslmayr, 2007) or even the inhibition of information (Händel et al., 2011). For example, when visual stimuli are presented to the right and left side but participants are asked to respond to the stimulus

[10] Task during which participants react to a simply stimulus consecutively. This is randomly interrupted by the presentation of a deviant stimulus and participants need to avoid responding on these trials.

on the left and ignore the stimulus on the right side, alpha synchronization is found in left posterior regions, whereas alpha desynchronization is found in right posterior regions. This is because the irrelevant stimulus in the right hemifield is processed by left posterior regions, which show increased alpha synchronization to suppress the irrelevant information so that stimuli in the relevant visual field can be processed without interference (Händel et al., 2011).

During action execution, alpha desynchronizes over central and parietal areas. This has been attributed to the activity of motor and sensorimotor areas (Fox et al., 2016; Hobson & Bishop, 2017) and has been referred to as the mu frequency. Among others, mu occurs during the observation and execution of actions. Therefore, it has been linked to MN activity, which is important when examining the neural correlates of automatic imitation.

1.1.11 Mu rhythm and the processing of biological stimuli

Henri Gastaut discovered the mu rhythm in 1952. It was first named the rolandic wicket rhythm since it was discovered over rolandic (central) areas and had a wicket or arched shaped oscillation in the alpha range (8-12 Hz), due to the contribution of alpha and beta frequencies. Gastaut first assumed that the mu rhythm was an indicator of human disability since it was increasingly found in subjects with psychological abnormalities. However, as the methodology improved, mu was observed in the majority of the participants and became associated with active and passive movements (Chatrian, Petersen, & Lazarte, 1959). More importantly, Gastaut and Bert (1954) observed mu desynchronization during both self-executed and observed movements. Hence, mu activity exhibited similar features as MNs discovered in macaque monkeys (Fogassi et al., 2005; Gallese, 1996), which fuelled research mapping the human MN system using mu activity.

Two recent reviews have assessed whether mu activity is a reliable measure to assess the MN system (Fox et al., 2016; Hobson & Bishop, 2017). Despite similar evidence, both reviews arrived at different conclusions. Fox et al. (2016) derived a positive conclusion whereas, Hobson et al. (2017) adopted a more critical perspective. Both reviews mentioned that most studies suffered from small sample sizes, which could increase the false positive rate of the reported findings. Further, the mu frequency band was not consistent throughout experiments. Whereas some studies used 8-12 Hz (Perry & Bentin, 2010),

8-13 Hz (Perry, Stein, & Bentin, 2011), 8-16 Hz (Tamura et al., 2012) others separated the frequency band into distinct alpha and beta components (Hari et al., 1998). Since alpha and beta frequencies vary between people, it is possible that mu also varies between people (Thorpe, Cannon, & Fox, 2016). Therefore, the mu frequency band can vary between studies as well. More importantly, studies recording mu activity focus on pre-selected electrodes in central areas with no subsequent source localization. Therefore, it is difficult to know whether the changes picked up by central channels are being generated in more distant regions. Lastly, mu activity should be unaffected by attention whereas alpha changes with attentional demands (Hobson & Bishop, 2017). However, most studies have not provided evidence whether attention influenced the measured mu activity or not. Without proper control conditions and the ability to differentiate the posterior alpha from central mu activity the usage of mu activity to assess the human MN system needs to be taken with caution. That being said, many studies have focused on mu activity during imitation and revealed exciting results, which will be discussed further in Chapter 5.

1.1.12 The general function of beta activity

Beta activity (13-30Hz) is often recorded from sensorimotor areas (Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008; Hari et al., 1998; Jenkinson & Brown, 2011). The beta band typically desynchronizes before a movement and synchronizes after the movement has finished (Zaepffel, Trachel, Kilavik, & Brochier, 2013). Beta oscillations are picked up by tissue surrounding the neurons and measured in the form of microtremors in muscle fibres (Kilner et al., 1999). Hence, beta oscillations can be measured non-invasively from the muscle tissue as well as through EEG and MEG recordings. EEG, MEG or physiological studies suggest that increased beta synchronization in motor areas such as the M1 slows down voluntary movements, whereas increased desynchronization facilitates voluntary movements (Gilbertson, 2005; Pogosyan, Gaynor, Eusebio, & Brown, 2009). This is supported by research applying beta entrainment to the M1 to prolong RTs (Pogosyan et al., 2009).

The ease of response execution also influences beta band power in central and parietal areas: less beta desynchronization is observed if the uncertainty of the to-be-performed

response is high: e.g. by pre-cueing multiple target locations instead of a single location (Tzagarakis, Ince, Leuthold, & Pellizzer, 2010). Similarly, more beta desynchronization in frontoparietal areas is observed when a response is repetitive instead of changing and more demanding (Park, Kim, & Chung, 2013). In sum, beta power is decreased when easy actions are voluntarily executed and increased when tonic postures are maintained. However, these results contradict findings that beta desynchronization increases in visual search tasks throughout the dorsal stream (visual, parietal and frontal areas) as a marker of increased cognitive effort (Gola, Magnuski, Szumska, & Wróbel, 2013; Siegel, Donner, Oostenveld, Fries, & Engel, 2008). This could indicate the beta activity related to movement, and visual attention show different activity signatures.

1.1.13 Conclusion and present studies

In conclusion, the present introduction has illustrated that humans automatically copy the behaviour of others in a variety of social settings. The effect has been termed motor mimicry and has been related to important social outcomes such as empathy and liking. Automatic imitation is said to be related to motor mimicry since both processes are unintentional and unconscious (Heyes, 2011). S-R, simple-response or simple-response kinematic-movement paradigms have been used to study automatic imitation. All paradigms show that a compatible/congruent biological stimulus facilitates behaviour whereas an incompatible/incongruent biological stimulus interferes with behaviour. According to the ideomotor theory, these effects are based on an automatic mapping of the observed behaviour onto the observer's motor system by anticipation of the action outcome (James, 1890). Importantly, this theory not only applies to biological but also to spatial stimuli. Spatial stimuli also trigger congruency effects, which suggests that spatial and biological stimuli are processed alike. However, still, there are proponents arguing that biological stimuli are processed more automatically than spatial stimuli (Scheutz & Bertenthal, 2012). This theory has got supporting evidence with the recent finding from Boyer et al. (2012) that spatial but not biological stimuli trigger a reversed congruency effect. This means that the task instructions influence task-irrelevant spatial stimuli, whereas task-irrelevant biological stimuli are unaffected. Instead, biological stimuli are directly mapped onto the observer's motor system leading to imitation. This theory is

according to the direct-matching model of Sauser and Billard (2006).

The study from Boyer et al., (2012) did not include limitations found in other S-R paradigms addressed above. However, the study used a between-subject design so that the SCy and BCy effects were not elicited in the same participant. Although statistical procedures can account for between-subject variability, it is necessary to replicate the findings using a within-subject design to affirm that the differences between spatial and biological stimuli were not due to differences between groups. Secondly, Boyer et al. (2012) only used a blocked design, in which participants either performed an S-R or an OS-R task. It has been suggested that participants can form response strategies in blocked designs (e.g. blur the vision), which can help them respond quicker but at the same time can distort the results (Catmur & Heyes, 2011). These strategies can differ between spatial and biological tasks and hence trigger different outcomes for different types of stimuli. Lastly, congruency and reversed congruency effects, which are calculated by subtracting the RTs in the congruent condition from RTs in the incongruent condition, are very small (approximately around 20 ms, (Boyer et al., 2012; Press et al., 2005)). However, standard experimental equipment such as a computer screen can readily exhibit slight timing variations, which could affect such small effects. For example, monitor refresh rates get stuck and thereby increase the duration of the stimulus display by several milliseconds. What seems trivial at first can influence effects as small as the SCy and BCy effects. Therefore, it is necessary to ensure that the experimental set-up can detect such slight variations in timing so that the affected trials can be excluded.

Four behavioural experiments will therefore be set-up, which address these limitations of Boyer et al (2012) to gain a better understanding whether spatial and biological S-R mappings follow the single or the direct-matching model (Sauser & Billard, 2006). The paradigm of Boyer et al. (2012) was replicated but Experiment 1 assessed SCy and R-SCy effects using a within-subject design. Experiment 2, replicated Experiment 1 but used a mixed instead of a blocked design. Experiment 3 and 4 replicated Experiment 1 and 2 but assessed BCy and R-BCys effects. In all four experiments an experimental set-up was used to detect refresh rate errors and exclude the affected trials. If the single route model is true, then spatial and biological cues would be processed in the same routes. This would mean that task irrelevant biological and spatial stimuli would show the same

behavioral results. More specifically, both task irrelevant stimuli would be influenced by S-R mappings established by the task instructions. This would result in a congruency effect in the S-R tasks and a reversed congruency effect in the OS-R tasks. If the direct-matching model is true, then task irrelevant biological and spatial stimuli are processed in different routes. Task irrelevant spatial stimuli would be influenced by the S-R mappings established by the task instructions. This would trigger as SCy effect in the S-R task and a reversed SCy effect in the OS-R task. Since biological stimuli are directly mapped onto the participants' motor system regardless of the stimulus-response mapping induced by the task instruction, task irrelevant biological stimuli should trigger a BCy effect in the S-R and the OS-R tasks (for a schematic view of these hypotheses see, Figure 3) (Sauser & Billard, 2006).

		Task irrelevant biological stimuli (Experiment 3 and 4)	**Task irrelevant spatial stimuli (Experiment 1 and 2)**
Single-route model	**S-R task**	Congruency effect Activity outside MN areas e.g. PPC	Congruency effect Activity outside MN areas e.g. PPC
	OS-R task	Reversed congruency effect Activity outside MN areas e.g. PPC Reversed neural congruency effect	Reversed congruency effect Activity outside MN areas e.g. PPC Reversed neural congruency effect
Direct-matching model	**S-R task**	Congruency effect Activity in MN areas e.g. IFG	Congruency effect Activity outside MN areas e.g. PPC
	OS-R task	Congruency effect or null finding Activity in MN areas e.g. IFG No reversed neural congruency effect	Reversed congruency effect Activity outside MN areas e.g. PPC Reversed neural congruency effect

Figure 3: The table shows the predictions of the Single-route and Direct-matching models in the S-R and OS-R tasks for task irrelevant spatial and biological stimuli.

Since behavioural studies only provide indirect evidence for neural mechanisms it has been necessary to investigate the neural underpinnings of automatic imitation. To date, much research has focused on MNs and how these neurons might facilitate imitation. TMS and fMRI studies have found evidence that automatic imitation triggers activity in areas associated with MN activity. However, TMS has a reduced spatial resolution, whereas

fMRI suffers from poor temporal resolution. Since MEG has an excellent temporal and a good spatial resolution when combined with a structural scan, MEG should be used to examine which neural processes lead up to the facilitation and inference effects during automatic imitation or the spatial equivalent.

Therefore, two additional MEG experiments have been set-up to assess the neural processes leading up to automatic imitation and SCy effects. This will ultimately answer whether biological cues are processed in a single route (Sauser & Billard, 2006), which relies on MN areas to trigger imitation. If the single route model is true, spatial and biological task irrelevant stimuli should use similar neural networks. In the S-R tasks one should therefore observe similar mechanisms inhibiting the response to the task irrelevant biological/spatial incongruent cues. In the OS-R tasks, the reversed mapping rule should trigger a reversal of the neural effect shown in the S-R tasks. Accordingly, the areas, which inhibited the task irrelevant incongruent stimuli in the S-R tasks should inhibit the task irrelevant congruent stimuli in the OS-R tasks (reversed neural congruency effect). If the direct-matching model is true spatial and biological stimuli are processed in different neural networks. Whereas spatial stimuli should be processed in hubs for spatial attention (e.g. PPC) biological stimuli should be processed in mirror neuron areas such as the IFG, including the vPMC and pars opercularis (PO). Further, a reversed neural congruency effect should only be observed for task irrelevant spatial stimuli, since biological stimuli are not influenced by the switch in the S-R mapping rule caused by the change in task instructions between the S-R and OS-R tasks (Figure 3).

These results will provide answers to the question whether humans have developed a MN network to promote social interaction.

2 Chapter 2

2.1 Introduction – Experiment 1 and 2

When a stimulus is unconsciously paired with a specific response, it becomes a S-R contingency/mapping (Eimer, 1995). Whenever the same stimulus is encountered it triggers the associated response, although it might interfere with task performance (R. K. Ridderinkhof, 2002). Many such S-R pairings exist, and they are used in a wide variety of contexts to teach and learn behaviour (Balleine & Dickinson, 1998). In the General Introduction biological and spatial S-R contingencies were described, since the current line of work aims at answering whether biological S-R contingencies are processed differently from the spatial equivalent. Spatial stimuli can automatically elicit actions, but deliberate processes control such automatic mechanisms. That is, depending on the situation, the learned spatial S-R mapping is applied, but response rules, which are determined by task instructions can influence it (R. K. Ridderinkhof, 2002). Currently, it is under debate whether biological stimuli are processed alike. To date, the leading theories such as the ideomotor theory, the common coding theory and the dimensional overlap model explain spatial and biological S-R mapping similarly (James, 1890; Kornblum et al., 1990; Prinz, 1990). With slight variations, all theories (models) propose that perceived sensory stimuli trigger action goals (metalization of the outcome of an action), which elicit actions. The more the observed sensory stimuli and the mentalized action-goal contain overlapping features, the higher the probability that sensory information triggers an action. However, it has been proposed that internalized biological S-R mappings in contrast to their spatial counterparts cannot be influenced by response rules, which form short-term S-R associations. This means that observed biological stimuli always trigger imitation (Chartrand & Bargh, 1999). In order to determine whether biological stimuli are processed uniquely, it is essential to understand generic S-R mapping mechanisms. The leading theories and experiments concerning spatial S-R mappings were already explained in the General Introduction. The following paragraphs will refer to these topics and provide more in-depth

information so that the reader will form a thorough understanding of what spatial S-R contingencies are, and how they can be differentiated from the biological equivalent.

2.1.1 Original paradigms measuring the simon effects

The Simon effect was introduced in the General Discussion as a non-biological (spatial) S-R mapping (Simon, 1969; Craft & Simon, 1970; Simon, Acosta, Mewaldt, & Speidel, 1976). As BCy effects, the spatial equivalent is elicited in an S-R paradigm. The Simon effect has been widely studied since 1969 and has been elicited using a wide variety of stimuli such as tones, visual stimuli presented on a computer monitor, objects and directional words (Proctor, Miles, & Baroni, 2011; Hommel, 2011). All of these experiments and their results share common features. As in the original experiments by Simon et al. (1969; 1970), an imperative task-relevant stimulus is presented (e.g. colour). The participants are asked to make a matching response to that stimulus (e.g. press one of two response buttons with the matching colour). Importantly, the stimulus incorporates a task-irrelevant feature as well (e.g. right/left location of the stimulus), which influences the response. If the task-irrelevant feature is spatially-congruent (e.g. the response button is on the same side as the presented stimulus), response times are faster and less erroneous. If the task-irrelevant feature is spatially-incongruent (e.g. the response button is on the opposite side as the presented stimulus), response times are slower and more erroneous. Hence, the task-irrelevant spatial dimension influences response speed and response accuracy.

2.1.2 Learned S-R associations and the role in spatial S-R mapping

In the General Instruction the ideomotor theory, common coding theory and the dimensional overlap model were explained to understand why SCy and BCy effects occur (James, 1890; Kornblum et al., 1990; Prinz, 1990). All theories suggest that the mentalizing of action-consequences trigger action-execution and that sensory information can trigger the mentalization of action-goals. Here, empirical evidence is provided to show that links

between action and action-consequences can be learned and that the appearance of sensory information, which resembles an action-consequence, triggers the associated movement. For example, Elsner and Hommel (2001) let participants freely produce two distinct key-presses, which resulted in two different sounds (high-pitched vs low-pitched sound). Therefore, key-press 'A' was related to sound 'A' and key-press 'B' was associated with sound 'B'. Later, participants heard the same sounds and freely chose to press button 'A' or 'B' afterwards. Consistently, participants pressed the button more often, which had been paired with the sound in the previous task. Hence, participants had formed bi-directional 'action to action-consequence' associations in the first task, which were used in the second task to choose the response. This result was supported by imaging studies showing that a tone, which has been paired to a movement previously, triggers activation in movement-related areas (e.g. SMA) when being presented by itself (Elsner et al., 2002; Melcher, Weidema, Eenshuistra, Hommel, & Gruber, 2008). These experiments show that actions are linked to their sensory consequences and that the perception of sensory information can trigger the mentalization of an action-goal, which in turn triggers the actual movement. These connections have also been termed long-term S-R associations since they are learned by experience and strengthened over time (Tagliabue et al., 2000). The question will be whether such long-term associations are more persistent for biological cues than for spatial cues, since it has been shown that spatial long-term S-R associations can be inhibited easily.

2.1.3 The reversed Simon effect

The R-SCy effect in the OS-R task is elicited by a change in the response rule determined by the task instructions, which reverses the SCy effect (See, General Introduction) (Hedge & Marsh, 1975). When participants are instructed to respond in a compatible manner to the imperative stimulus a SCy effect occurs. However, when told to respond in an incompatible manner a R-SCy results.

The dimensional overlap and common coding theories would have predicted a SCy ef-

fect regardless of the task requirements since the congruent stimulus always shares more features with the response than the incongruent stimulus. To date, the R-SCy effect has been replicated repeatedly (De Jong, Liang, & Lauber, 1994; Hasbroucq & Guiard, 1991). Although the mechanisms behind the R-SCy effect (e.g. logical recoding; See, General Introduction) are still under debate, the effect shows that long-term associations between observed stimuli and executed actions can be influenced by short-term S-R associations defined by the task instructions (R. K. Ridderinkhof, 2002). This is of out-most importance, since biological long-term S-R associations seem to be more stable (Bertenthal, Longo, & Kosobud, 2006).

2.1.4 Automatic and deliberate processes contributing to the SCy effects

Dejong (1994) suggested that short-term S-R associations caused the R-SCy effect but that this did not weaken the importance of long-term automatic mechanisms for the Simon effect. To prove this, participants performed S-R and OS-R tasks and as expected the former triggered a SCy effect whereas the latter revealed a R-SCy effect. A distributional analysis (Ratcliff, 1979) was subsequently used to gain insights into the timing of the automatic (long-term associations) and the deliberate (short-term associations) processes, which potentially caused the effects. Responses on spatially-congruent and spatially-incongruent trials were separated and divided into five time bins (from fastest to slowest RTs). For each time bin, the Simon effect was calculated by subtracting the mean-RTs of the spatially-congruent conditions from the mean-RTs from the spatially-incongruent conditions, and the resulting distributions (delta plots) depicted the SCy and the R-SCy effects over time. In the S-R task, the SCy effect decreased with time, reaching zero in the last two time bins. The R-SCy effect in the OS-R task was smallest with fast RTs and increased afterwards. According to Dejong (1994), these differences between slopes in the delta plots of the S-R and OS-R tasks suggested that the SCy effect in the S-R task employed long-term S-R association, whereas short-term S-R associations evoked the R-SCy effect in the OS-R task.

These conclusions can best be explained by the action-suppression model (R. K. Ridderinkhof, 2002), which is based on the dimensional overlap model (Kornblum et al., 1990). It suggests that automatic processes trigger congruent responses by employing long-term S-R associations. A deliberate route processes the task-relevant information and executes the response using short-term S-R associations, which are based on task instructions. Whereas the automatic route is fast since it relies on previously learned behaviour, the deliberate route is slower since it forms the S-R mapping instantaneously. The deliberate route can override the information from the automatic route. However, since the deliberate route is slower than the automatic route, fast responses reveal a bias towards the congruent response before the deliberate route controls these responses if necessary (R. K. Ridderinkhof, 2002). This means that fast responses are guided by long-term S-R associations whereas slow responses are in line with the short-term S-R associations.

Further, it was suggested that a distributional analysis (Ratcliff, 1979) can provide insights on the deliberate and automatic processes contributing to the SCy and R-SCy effects, since it provides information about the speed of the processes underlying these effects (R. K. Ridderinkhof, 2002; K. R. Ridderinkhof, van den Wildenberg, Wijnen, & Burle, 2004). Most experiments assessing the Simon effect, using the original paradigm explained above, show that the SCy effect is largest with fast RTs and becomes smaller with increasing RTs. This decreasing trend of the SCy effect is attributed to the influence of the deliberate route, which progressively inhibits the fast, automatic and congruent responses elicited by long-term S-R associations. Accordingly, less facilitation or interference effects from the task-irrelevant spatial stimulus occur with time, which gradually decreases the SCy effect.

By increasing the influence from the deliberate route, Ridderinkhof (2002) elicited a R-SCy effect for longer RTs in an S-R task. Participants performed Simon-like S-R tasks where the imperative stimulus was a colour-cue, and the task-irrelevant stimulus was the spatial (right/left) location of this colour-cue. In one experiment 75% of the trials were

spatially-incongruent, whereas another experiment incorporated 75% spatially-congruent trials. He suggested that the former experiment induced more control from the deliberate route since the automatic congruent response was less beneficial overall. In the experiment with more spatially-incongruent trials, a R-SCy effect was revealed when RTs were longer than 350 ms. This suggests that automatic long-term S-R associations were working when RTs were below 350 ms. However, these were influenced by the deliberate short-term S-R associations with increasing time. In contrast, the experiment with more spatially-congruent trials revealed a SCy effect, which gradually increased, suggesting that the automatic and deliberate routes supported the spatially-congruent response, since it was more likely correct.

Further, Ridderinkhof (2002) assessed how an incorrect response on the previous trial affected the contribution of automatic and deliberate processes on the current trial. It was suggested that an error on the previous trial increased the activity of the deliberate route, which increased the inhibition of the automatic route on the current trial. This manipulation only affected responses in the experiment with more spatially-congruent trials. Here, post-error trials revealed a SCy effect for fast responses, which flipped into a R-SCy effect for slower responses. It was suggested that deliberate processes inhibited the congruent response increasingly with slower RTs. In all, the results showed that a distributional analysis can be used to gain insights into the mechanisms triggering congruency effects by depicting whether the effects are caused by fast are slow mechanisms.

Returning to the results from Dejong (1994), which showed that the SCy effects in the S-R task decreased with time, and that the R-SCy effects increased with time. According to the action-suppression model, this would indicate that the SCy effect in the S-R task was guided by fast, automatic long-term S-R associations, which were elicited quickly and later influenced by short-term S-R associations. In contrast, the R-SCy effect was guided by deliberate short-term S-R associations, which build-up with slower RTs. Hence, the presence of the R-SCy effect in the OS-R task did not contradict the predictions of the ideomotor theory. It only showed that 'suppression' from a deliberate route influenced the

learned long-term S-R associations in the OS-R task. This is important since biological stimuli are not affected alike (See Introduction - Experiment 1 and 2).

2.1.5 How RT variability can influence delta plots

Some doubt exists whether delta plots can give reliable insights into the timing of cognitive processes, since the slopes depend on the variability of the responses in the spatially-congruent and spatially-incongruent conditions: If the variance among RTs is higher in the congruent than in the incongruent condition, the slope of the delta plot decreases and vice versa (J. Zhang & Kornblum, 1997). Despite such concerns, delta plots have continuously been used, and a recent review concluded that delta plots could be used to understand the underlying cognitive processes in S-R tasks (Proctor et al., 2011). However, it is important to statistically test whether the variances of RTs in the congruent and incongruent conditions differ, to be aware of potential influences on the delta plots.

2.1.6 Explaining the contribution of deliberate processes during S-R mappings by the use of computational models

That deliberate processes can control the processing of spatial stimuli was also stressed in the computational models of Sauser and Billard (2006), which are described in the General Introduction. In both of their models (direct-matching model and single-route model) task-irrelevant spatial stimuli are processed in an S-R mapping stage, which is influenced by 'deliberate' input from the PFC. Task-irrelevant biological stimuli are processed similarly to spatial stimuli in the single-route model. Conversely, the direct-matching model includes an additional route for perceived biological stimuli, which receives no input from the PFC. Therefore, it elicits imitation regardless of the task. Since both models predict a congruency effect for task-irrelevant spatial and biological stimuli in the S-R task, the contribution of deliberate processes can only be assessed using an OS-R task. Here the single-route model predicts R-SCy and R-BCy effects. However, since the direct-matching model simulates how task-irrelevant biological stimuli are processed without the contri-

bution of deliberate mechanisms, the model only predicts a R-SCy effect.

As noted in the General Introduction, Boyer et al.(2012) used a novel design to test the predictions of the single-route and direct-matching models. The paradigm was based on an earlier study of Bertenthal et al., (2006). A right or a left hand in a third person perspective was presented on the screen. This hand could either tap with the index or middle finger. Participants responded by tapping the middle or the index finger of their right hand as soon as they detected a movement on the screen. In the biological S-R (bS-R) task, which measured the SCy effect, the participants were asked to identify the actor's tapping finger (middle finger vs index finger) and respond in accordance with it. If the actor tapped the index finger, the participant responded with an index finger tap as well. If the actor tapped the middle finger, the participant responded with a middle finger tap. SCy was manipulated by switching between the presentation of right or left hands. If a left hand was shown responses were spatially-congruent (the stimulus-hand and the participant moved the finger on the same side) and if a right hand was shown responses were spatially-incongruent (the stimulus-hand and the participant moved fingers on different sides). Additionally, a biological OS-R (bOS-R) task was added, in which participants responded with the non-matching finger (e.g. responding with a middle finger tap when an index finger tap was observed). If a right hand was shown responses were spatially-congruent, and if a left hand was shown responses were spatially-incongruent. In the spatial S-R (sS-R) task, which measured automatic imitation, the participants were asked to identify in which hemifield the tapping finger was presented (right vs left) and respond in accordance with it. If the actor tapped the finger on the right side, the participants tapped with the middle finger [11]. If the actor tapped the finger on the left side, the participants tapped with the index finger [12]. If a left hand was presented responses were biologically-congruent (the stimulus hand and the participants moved the same finger) and if a right hand was shown responses were biologically-incongruent (the stimulus hand and the participants moved different fingers). A spatial OS-R (sOS-R)

[11]Since the middle finger of the right hand is to the right of the index finger.
[12]Since the index finger of the right hand is to the left of the middle finger.

task was added, in which participants responded with the finger that was spatially non-matching to the finger tapping on the screen (e.g. making a right side/middle finger tap when an index finger tap with the left hand was observed). If a right hand was shown responses were biologically-congruent and if a left hand was shown responses were biologically-incongruent. A SCy and a R-SCy effect were revealed the bS-R and bOS-R tasks respectively. A BCy effect was also revealed in the sS-R task, but no effect was observed in the sOS-R task. The results were in line with the direct-matching model, which predicted that only spatial S-R mappings are influenced by deliberate S-R processes, whereas biological stimuli are directly mapped onto the observer's motor system (Sauser and Billard, 2006). In other words, the study showed that biological task-irrelevant stimuli are processed without the same amount of interference from short-term S-R mappings as observed for task-irrelevant spatial stimuli.

2.1.7 Potential factors that could have influenced the results of Boyer et al. (2012)

Although the study of Boyer et al. (2012) did not include any of the limitations usually found in S-R paradigms (see, General Introduction), three factors could potentially have influenced the results. The study used a between-subject design in which one group of participants performed the spatial tasks, whereas the second group performed the biological tasks. Hence, the observed results could be due to differences in group characteristics. Although statistical testing takes between-group variations into account, within-subject experiments, in which all subjects perform all tasks have higher internal validity (Charness, Gneezy, & Kuhn, 2012). Therefore, it is necessary to replicate the study of Boyer et al. (2012) using a within-subject design, to confirm that the differences between spatial and biological task-irrelevant stimuli were not due to differences between groups.

Secondly, Boyer et al. (2012) only used a blocked design, in which participants either performed an S-R or an OS-R task within one block. Hence, subjects never had to change the task but could focus on one type of response throughout an experimental

block. In blocked experiments, participants can form response strategies (e.g. blur the vision), which can influence how they respond to the presented stimuli (Catmur & Heyes, 2011). These strategies can differ between spatial and biological tasks and trigger different outcomes for different types of stimuli. Most of the studies assessing the SCy and the R-SCy effects have used blocked designs (Brass et al., 2000; Hedge & Marsh, 1975). However, both effects have shown to be very consistent in more demanding experiments using a mixed design. In such experiments, the participants are told to execute different responses depending on a pre-cue. For example, Dejong (1994) randomly varied S-R and OS-R tasks within the same block. Therefore, it was impossible to form predefined expectations about the task since repeated task switching was necessary. Despite such increased difficulty the SCy and the R-SCy effects remained. In other experiments, S-R and OS-R tasks were mixed with spatial compatibility tasks within the same block. [13] In these experiments the SCy and the R-SCy effect remained, whereas the spatial compatibility effect was abolished (Proctor and Vu 2002; Marble and Proctor., 2000). This shows that SCy and R-SCy effects in S-R and OS-R tasks are not influenced by mental effort (Proctor & Fisicaro, 1977), response uncertainty and inter-trial variability (Los, 1996). Mixed designs have the advantage that no predefined response strategies can be employed (e.g. blurring vision), which in turn could mediate the observed effects (Catmur & Heyes, 2011). Hence, using mixed in addition to blocked designs is beneficial to test the validity of the SCy and the R-SCy effects as well as the biological equivalents assessed in the following chapter.

The last very important issue, which needs to be considered when testing the reliability of the results from Boyer et al. (2012) is the accuracy of the experimental set-up. As outlined in the General Introduction, congruency and reversed congruency effects, which are calculated by subtracting the RTs in the congruent condition from RTs in the incongruent condition, are in the millisecond range (Press et al., 2005; Boyer et al., 2012).

[13] In spatial compatibility tasks, participants see a stimulus on the left or right side of the screen and are asked to respond to that spatial stimulus. RTs are faster when participants are told to respond in a spatially compatible (e.g. pressing the response key on the same side as the stimulus) in comparison to a spatially incompatible manner (e.g. pressing the response key on the opposite side as the stimulus).

Therefore, these effects can be distorted by fluctuations in the monitor refresh rate. The current study used a set-up, which detected and excluded the affected trials to increase the accuracy of the revealed results.

2.1.8 Aim of the study

The present introduction gave an overview about spatial S-R contingencies with the main focus on the action-suppression model, which shows that deliberate processes can control learned and automatic spatial S-R associations. This is very important since it could distinguish between the processing of spatial and biological stimuli. The main objective of the present line of work is to answer the question whether humans have developed a unique cognitive mechanism to process biological cues by directly mapping the observed stimuli onto the observer's motor system so that imitation is facilitated. By having reviewed the literature about SCy effects, it is now apparent that spatial cues can be 'mapped' directly onto the observer's motor system but that this mechanism can be controlled by more deliberate processes. If it is true that biological stimuli are not affected by such deliberate processes, there is a clear distinction between the processing of biological and spatial stimuli. However, before assessing the unique nature of biological stimuli, it is important to know how generic non-biological S-R mechanisms function. Therefore, the present study is set-up to validate the findings in the bS-R and bOS-R tasks from the study of Boyer et al. (2012) to gain a better understanding about generic (non-biological) S-R mappings. This was done by addressing the potential factors described above, which could have influenced the results of Boyer et al. (2012). Lastly, the aim was to understand whether automatic and/or deliberate mechanisms underlie spatial S-R contingencies (Ratcliff, 1979). Boyer et al. (2012) also calculated delta plots. However, the results were not discussed in their paper, since they were skeptical whether the slope of the delta plots were influenced by the variance of the RTs in the congruent and incongruent conditions (J. Zhang & Kornblum, 1997). Here statistical testing of the differences in variance between conditions is added to test whether such differences could cause the

results observed in the delta plots. Secondly, an additional distributional analysis is added, in which errors in spatially-congruent and spatially-incongruent conditions are split into 5 time bins from fastest to slowest responses. Since the active-suppression model suggests that the automatic route acts fast, one should observe fast errors in accordance with the automatic route regardless of the task.

The first experiment uses a very similar experimental set-up as the bS-R and bOS-R tasks in Boyer et al. (2012) but with a within-subject design. Likely a SCy effect is observed in the bS-R task. According to the action-suppression model, the SCy effect should decrease with increasing reaction. More fast errors should be revealed in the spatially-incongruent condition in comparison to the spatially-congruent condition, which would indicate that participants have a fast tendency to respond in a spatially-congruent manner. In the bOS-R task one should observe a R-SCy effect, which should increase with increasing RT, due to the influence of deliberate processes. Lastly, more fast errors should be revealed in the spatially-incongruent condition in comparison to the spatially-congruent condition, due to the fast tendency to respond in a spatially-congruent manner.

2.2 Methods – Experiment 1

2.2.1 Participants

Twenty volunteers participated in this experiment (mean age = 19.6, sd = 0.8, females = 15). All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). After visual inspection of the data two participants appeared to respond very differently from the rest of the sample. Since these two participants had the potential to alter the results for the whole sample, but no apparent reason was found to exclude them, the results are shown for 18 participants as well as for 20 participants. Further the results of the 2 outliers are shown in the Appendix B Figure 32. On average 8 percent of trials were removed for the analysis due to slow or fast RTs or due to errors in the experimental set-up. Informed, written consent was received before participation, and the STEM ethics committee from the University of Birmingham approved the study.

2.2.2 Materials and apparatus

The stimuli from Boyer et al. (2012) were taken as the starting point for creating four movies, each beginning with the presentation of an image of a right or left hand viewed from a third-person perspective (Figure 4). The hand initially remained static for 550 ms before it performed a downward tapping movement with either the middle or index finger. This movement acted as the imperative stimulus and was split into eight frames (16.7 ms each) for a total duration of 133.3 ms. At the end of the movement, the finger remained in the downward position for a further 550 ms. In total, the hand image was shown for 1233 ms, and in between stimuli a blank, white screen appeared for 2000 ms. In the original position, the displayed hand had a horizontal visual angle of 13.04°and a vertical visual angle of 8.17°. At the end of the tapping movement, the moving finger was displaced downward by approximately 2.86°visual angle. The stimuli were programmed and controlled using Psychophysics Toolbox (PTB-3) MATLAB 2012b (The MathWorks, Inc., Natick, Massachusetts, United States) software.

Participants were seated 70 cm away from a Sony desktop monitor (16.9" screen, 60 Hz refresh rate). A custom made response box with two response buttons was placed in front of the participants at the centre of the monitor. Participants positioned the middle and the index finger of their right hand on separate response buttons. Responses were captured by a Micro 1401 analogue-digital converter and recorded by Signal 6.01 software (both Cambridge Electronic Design, Cambridge, UK). A LabJack U3 connecting the experimental computer and the Micro 1401 allowed for sending digital inputs to Signal 6.01 (CED) that coded the condition of each trial. To ensure correct timing a photodiode was placed at the right bottom corner of the screen and connected to the Micro 1401. A square located in the bottom of the monitor recorded changes in luminance according to the position of the imperative stimulus, and this was measured by a photodiode (time resolution of 0.5 ms).

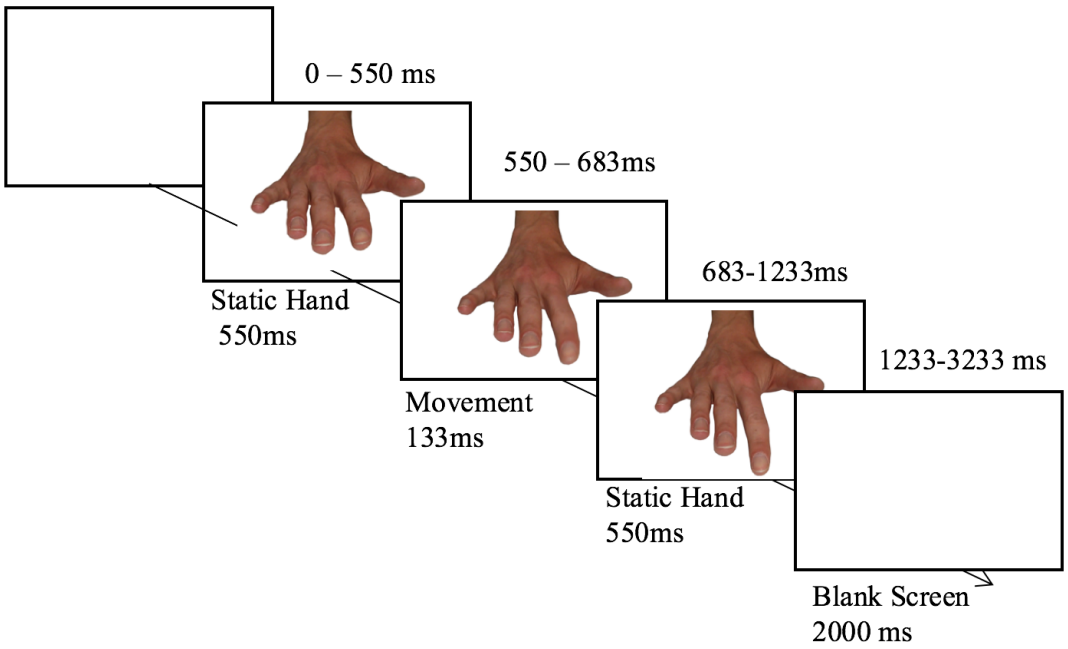


Figure 4: The time line of Experiment 1 (as well as Experiment 3 in Chapter 3). A trial began with a blank screen (2000 ms). Then the stationary hand in a neutral position was shown (550 ms). Next, 8 successive frames (133 ms) created the impression of a tapping movement of the index or middle finger. Lastly a static hand in the end position was shown (550 ms). Participants could respond as soon as the hand on the screen started moving (0 ms).

2.2.3 Procedure and design

The current experiment utilized the bS-R and bOS-R tasks implemented by Boyer et al. (2012) with the critical distinction that these tasks were administered to all participants using a within-subject design (Figure 4). Participants observed a hand performing a movement with the middle or index finger. They were instructed to take a third person perspective and to respond to identify the finger, which was tapping on the screen (middle vs index finger). Responses were executed by tapping with the middle or index finger of their right hand.

The bS-R task followed the logic of an S-R paradigm. Participants were instructed to respond according to the identity of the tapping finger on the screen (e.g. if the stimulus tapped with the index finger participants needed to tap with their index finger as well). SCy was manipulated by using left or right hands as stimuli. If a left hand was shown, all responses were spatially-congruent. If a right hand was shown, all responses were

spatially-incongruent.

The bOS-R task followed the logic of the OS-R paradigm. Participants were instructed to respond with the finger that did not match the finger tapping on the screen (e.g. if the stimulus tapped with the index finger participants needed to tap with their middle finger). Again, SCy was manipulated by using both left and right hands as stimuli. If a right hand was shown, all responses were spatially-congruent. If a left hand was shown, all responses were spatially-incongruent.

Before starting the experiment, verbal instructions were given and practice trials were administered until the experimenter could verify that the participants understood the procedure. The experiment was split into two blocks, one for each task. This was counterbalanced across participants. Each block consisted of 200 trials of which 100 trials were spatially-congruent, and 100 trials were spatially-incongruent. Participants were allowed a short break after every twenty trials.

2.2.4 Analysis

RTs were measured from the onset of the observed finger movement to the onset of the button-press. RTs less than 200 ms or greater than 1500 ms were excluded from further analysis. This was chosen to allow the same cut-off in all experiments (for more details see, experimental design and analysis of Experiment 2). Trials were excluded if the observed movement was more than 1 ms outside the intended 133 ms duration.

Congruency effects: Since RTs did not follow a normal distribution, median RTs were calculated for the spatially-congruent and spatially-incongruent conditions of each task. A 2 x 2 repeated measures ANOVA with factors TASK (bS-R, bOS-R) and CONGRUENCY (spatially-congruent, spatially-incongruent) was conducted.

Error rate analysis: Individual error rates were calculated as the number of incorrect responses as a percentage of total responses. Mean percentage error rates were then calculated for all four conditions and a 2 x 2 RM ANOVA with factors TASK (S-R, OS-R) and spatial CONGRUENCY (spatially-congruent, spatially-incongruent) was applied.

Reaction time distribution: To examine the time course of the SCy effects a quintile analysis was performed (Radcliff, 1979). For each participant, RTs were split into quintiles starting from the shortest to the longest responses. SCy effects were calculated within each quintile by subtracting the median RT for the spatially-congruent condition from the median RTs from the spatially-incongruent condition. Positive values indicated SCy effects whereas negative values indicated R-SCy effects. RM ANOVA with TASK (bS-R, bOS-R) x 5 QUINTILE (quintiles 1-5) was subsequently applied to determine the effects of tasks and response time on this measure. Additional linear effects were analyzed within each condition (spatially-congruent, spatially-incongruent) for each task (bS-R, bOS-R) by using a RM ANOVA with QUINTILE (quintile 1-5) as factor.

Response accuracy distribution: To examine whether accuracy changed with RT length a quintile analysis was performed (Radcliff, 1979). For each participant RTs were split into quintiles starting from the shortest to the longest responses. Within each time bin the number of errors were divided by the number of all response and subsequently multiplied by 100. RM ANOVA with CONGRUENCY (spatially-congruent, spatially-incongruent) x 5 QUINTILE (quintiles 1-5) was subsequently applied to determine the effects of congruency and response time on this measure. Additional linear effects were analyzed within each condition (spatially-congruent, spatially-incongruent) for each task (bS-R, bOS-R) by using a RM ANOVA with QUINTILE (quintile 1-5) as factor.

Standard deviation analysis: Individual standard deviations were calculated for the spatially-congruent and spatially-incongruent conditions of each task. A 2 x 2 RM ANOVA with factors TASK (bS-R, bOS-R) and CONGRUENCY (spatially-congruent, spatially-incongruent) was conducted.

For all ANOVAs, the Greenhouse-Geisser (GG) correction was used if the assumption of sphericity was violated. Statistically significant main effects or interactions were explored with post-hoc sidak corrected tests. All statistical tests used an alpha level of 0.05. Statistical analysis was performed in IBM SPSS version 24 (IBM Corp. Released 2016. IBM SPSS Statistics for Macintosh, Version 24.0. Armonk, NY: IBM Corp.).

2.3 Results – Experiment 1

Two participants behaved very differently than the other 18 participants. However, since no objective criteria (e.g. number of errors or RT length) was found to exclude them the results are noted to 20 and 18 participants separately.

Congruency effects for 20 participants: RM ANOVA revealed a significant interaction between TASK and spatial CONGRUENCY, F(1,19)=80.09, p<0.001, η^2=0.81, and follow-up post hoc comparisons revealed that response times were faster during spatially-congruent trials in comparison to spatially-incongruent trials in the bS-R task (MD=43.7 ms, Std error = 6.3, p<0.001), whereas participants were faster during spatially-incongruent trials in the bOS-R task (MD=40.9 ms, Std error = 10.4, p<0.05; Figure 5A).

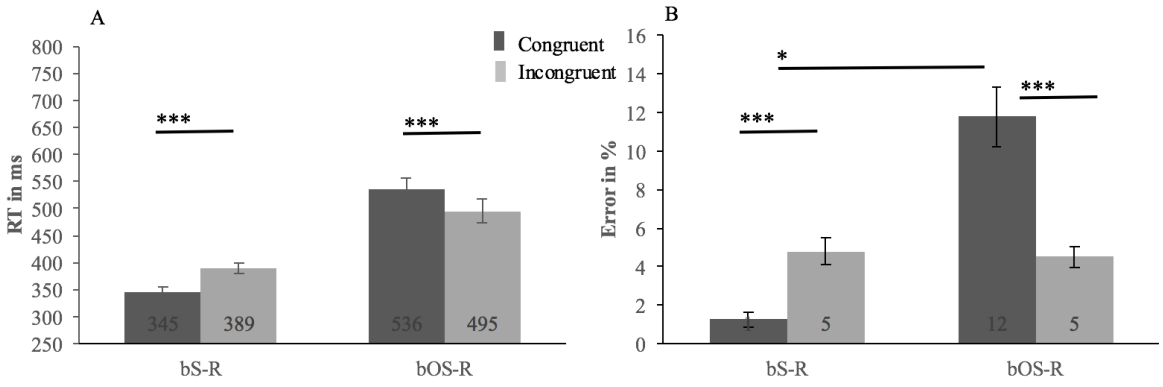


Figure 5: Shows the (A) RTs and (B) error rates in the bS-R and bOS-R tasks of Experiment 1 for 20 participants. In the bS-R task RTs were faster in the spatially-congruent condition than in the spatially-incongruent condition. This was reversed in the bOS-R task. In the bS-R task error rates were lowest in the spatially-congruent condition in comparison to spatially-incongruent condition. This was reversed in the bOS-R task.

Error rate analysis 20 participants: RM ANOVA with TASK and spatial CONGRUENCY as factors showed a significant main effect of TASK, F(1,19)= 5.61, p<0.05, η^2=0.23, indicating that participants made more errors in the bOS-R task in comparison to bS-R task (MD=5.2 %, Std error=0.7, p<0.001). A significant interaction, F(1,19)=29.23, p<0.001, 0.61, and post hoc tests revealed that participants made significantly more errors in the spatially-incongruent condition compared to the spatially-congruent condition

in the bS-R task (MD=3.6%, Std error = 0.7, $p<0.001$) and more errors in the spatially-congruent condition compared to the spatially-incongruent condition in the bOS-R task (MD=7.3%, Std error = 1.7, $p<0.001$; Figure 5B).

Reaction time distribution 20 participants: The RM ANOVA showed a significant main effect of TASK, $F(1,19)=24.61$, $p<0.001$, $\eta^2=0.56$ (Figure 6). No significant interaction between TASK and QUINTILE was revealed, $F(2,28)=1.79$, $p>0.05$, $\eta^2=0.08$ (GG). Anyhow, a linear effect was found in the sOS-R task, $F(1,19)=5.53$ $p<0.05$, but not in the sS-R task , $F(1,19)=0.004$ $p>0.05$. This indicates that the congruency effect systematically increased with increasing RT in the s0S-R task but not in the sS-R task.

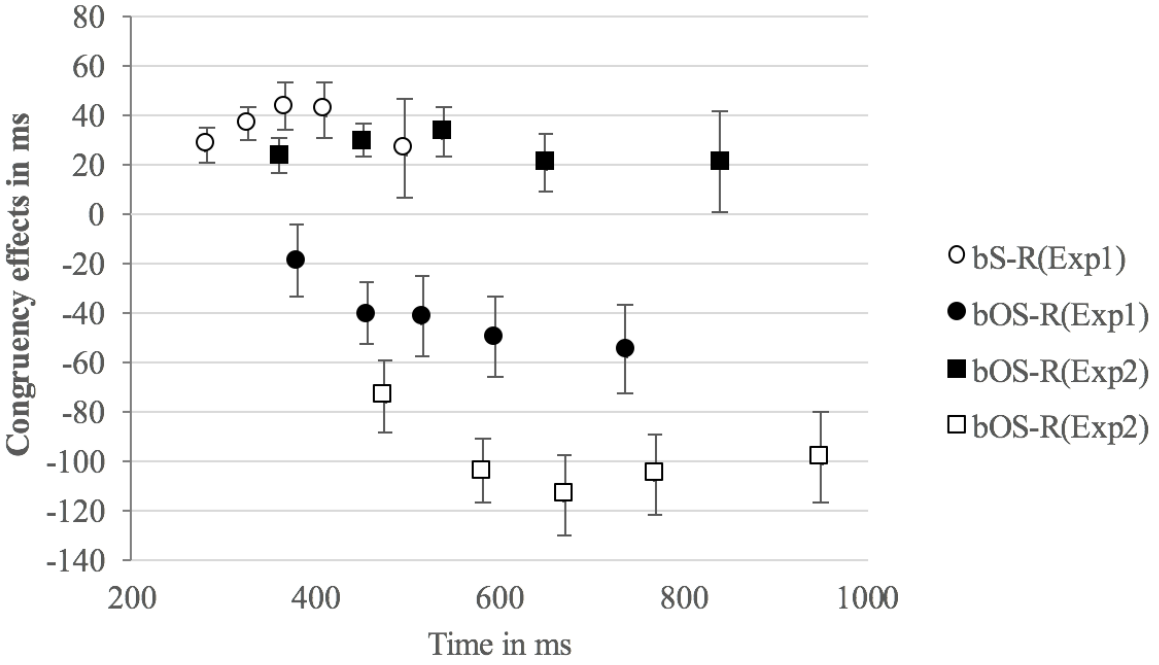


Figure 6: Shows the SCy and R-SCy effects in ms (y-axis) over RT-length (x-axis) from Experiment 1 (20 participants) and 2. In Experiment 1, the reversed SCy effect increased with increasing RT. In Experiment 2, a significant quadratic effect was observed in the bOS-R task. This indicated that the R-SCy effect increased with increasing RT but decreased again after the third quintile.

Response accuracy distribution bS-R task 20 participants: RM ANOVA showed a main effect of spatial CONGRUENCY, $F(1,19)=25.34$, $p<0.001$, $\eta^2=0.57$, a main effect of QUINTILE, $F(3,48)=5.44$, $p<0.01$, $\eta^2=0.22$ (GG), and a significant interaction

$F(4,76)=9.82$, $p<0.001$, $\eta^2=0.34$ (Figure 7). Post hoc tests indicated a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=7.5% , Std error = 1.9, $p<0.05$), second (MD=8.2 % , Std error = 1.3, $p<0.001$) and third (MD=1.8 % , Std error = 0.9, $p<0.05$) quintile. On all three occasions, participants made more errors on spatially-incongruent in comparison to spatially-congruent trials. In addition significant linear effects were found in the spatially-congruent, $F(1,19)=6.14$, $p<0.05$, and spatially-incongruent conditions , $F(1,19)=17.53$, $p<0.01$. Whereas the former showed more errors for slow responses the latter revealed more errors for fast responses (Figure 7).

bOS-R task: RM ANOVA showed a main effect of spatial CONGRUENCY, $F(1,19) = 18.96$, $p < 0.001$, $\eta^2=0.50$, a borderline effect of QUINTILE, $F(4,76) =2.41$, $p=0.056$, $\eta^2=0.11$, and a significant interaction $F(2,46)=7.34$, $p<0.05$, $\eta^2=0.28$ (GG). Post hoc tests indicated a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=11.3 % , Std error = 3.4, $p<0.05$), second (MD=13.1 % , Std error = 2.9, $p<0.001$) and third (MD=10.8 % , Std error = 2.3, $p<0.001$) quintile. On all three occasions, participants made more errors on spatially-congruent in comparison to spatially-incongruent trials. In addition significant linear effects were found in the spatially-congruent, $F(1,19)=10.93$, $p<0.01$, and spatially-incongruent conditions , $F(1,19)=4.64$, $p<0.05$. The former showed more errors for fast responses whereas the latter revealed the opposite effect (Figure 7).

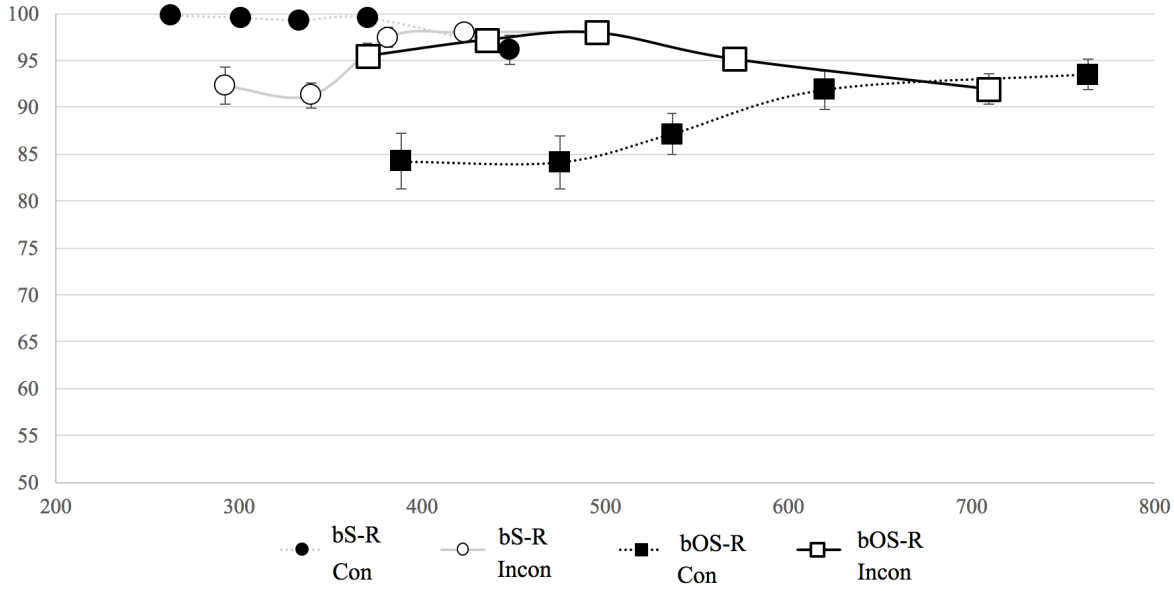


Figure 7: Shows the response accuracy in percentage (y-axis) over RT-length in ms (x-axis) from Experiment 1 for 20 participants. In the bS-R task more fast errors were made in the spatially-incongruent in comparison to spatially-congruent condition. This was reversed in the bOS-R task.

Standard deviation analysis for 20 participants: RM ANOVA with TASK and spatial CONGRUENCY as factors revealed a significant main effect of TASK $F(1,19)=46.35$, $p<0.001$, $\eta^2=0.71$, and a main effect of spatial CONGRUENCY, $F(1,19)= 9.72$, $p<0.01$, $\eta^2=0.34$, which indicated that more errors were made in the spatially-congruent in comparison to the spatially-incongruent conditions in both tasks. Further, no significant interaction was found, $F(1,19)=1.24$, $p > 0.05$, $\eta^2=0.06$ Figure 8).

	S-R		**OS-R**	
	Congruent	Incongruent	Congruent	Incongruent
Exp1 20 participants	95 ms	90 ms	158 ms	140 ms
Exp1 18 participants	80 ms	84 ms	151 ms *	139 ms *
Exp2	195 ms	189 ms	190 ms	182 ms
Exp3	56 ms	62 ms	80 ms	74 ms
Exp4	100 ms	108 ms	98 ms	98 ms

Figure 8: Shows the standard deviation from the congruent and incongruent conditions in the sS-R/bS-R and sOS-R/bOS-R tasks from Experiment 1 to 4. * indicates a significant difference between the variance of the RTs between the congruent and incongruent conditions in the respective tasks.

Above the results for 20 participants were presented. In the following sections the same analyses were performed for 18 participants.

Congruency effects for 18 participants: RM ANOVA revealed a main effect of TASK on response times, $F(1,17)=74.27$; $p<0.001$, $\eta^2=0.81$, indicating that participants responded faster in the bS-R task in comparison with the bOS-R task (MD=139.5 ms, Std error=16.2, $p<0.001$). A significant interaction between TASK and spatial CONGRUENCY, $F(1,17)=61.06$, $p<0.001$, $\eta^2=0.78$, and follow-up post hoc comparisons revealed that response times were faster during spatially-congruent trials in comparison to

spatially-incongruent trials in the bS-R task (MD=48.4 ms, Std error = 4.9, p<0.001), whereas participants were faster during spatially-incongruent trials in the bOS-R task (MD=46.2 ms, Std error = 9.1, p<0.001; Figure 9A).

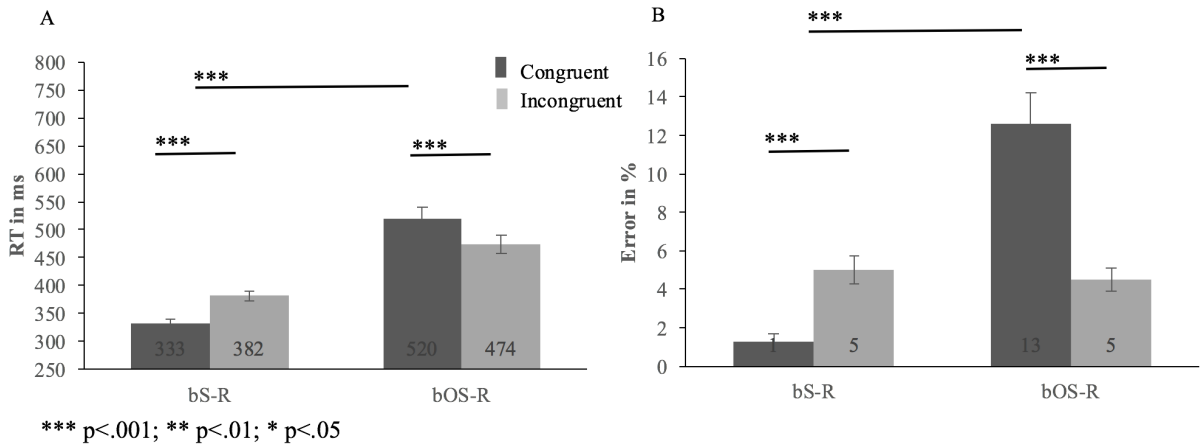


Figure 9: Shows the (A) RTs and (B) error rates in the bS-R and bOS-R tasks of Experiment 1 for 18 participants. In the bS-R task RTs were faster in the spatially-congruent condition than in the spatially-incongruent condition. This was reversed in the bOS-R task. In the bS-R task error rates were lowest in the spatially-congruent condition in comparison to spatially-incongruent condition. This was reversed in the bOS-R task.

Error rate analysis for 18 participants: RM ANOVA with TASK and spatial CONGRUENCY as factors showed a significant main effect of TASK, F(1,17)= 50.61, p<0.001, η^2=0.75, indicating that participants made more errors in the bOS-R task in comparison to bS-R task (MD=5.5 %, Std error=0.8, p<0.001). A significant interaction, F(1,17)=35.07, p<0.001, 0.67, and post hoc tests revealed that participants made significantly more errors in the spatially-incongruent condition compared to the spatially-congruent condition in the bS-R task (MD=3.8%, Std error = 0.7, p<0.001) and more errors in the spatially-congruent condition compared to the spatially-incongruent condition in the bOS-R task (MD=8.1%, Std error = 1.7, p<0.001; Figure 9B).

Reaction time distribution for 18 participants: The RM ANOVA showed a significant main effect of TASK, F(1,17)=75.02, p<0.001, η^2=0.82 (Figure 10). A significant interaction between TASK and QUINTILE was also revealed, F(2,29)=8.93, p=0.001, η^2=0.344 (GG). This indicates that the SCy effect in the bS-R task and the R-SCy effect

in the bOS-R task increased with increasing RT. This was confirmed by the borderline significant linear effect in the bS-R task, $F(1,17)=3.77$, $p=0.06$ and the significant linear effect detected in the bOS-R task, $F(1,17) = 13.91$, $p < 0.01$. Post-hoc comparisons revealed a significant difference between quintile one and four (MD=34.5 ms, Std error = 9.0, $p<0.05$) and between quintile one and five (MD=46.8 ms, Std error =11.4, $p<0.01$) in the bOS-R. Further, a significant difference was observed between quintile one and three (MD=8.3,Std error=4.4, $p<0.01$) and quintile one and four (MD=22.6, Std error=5.9, $p<0.05$) in the bS-R task (Figure 10).

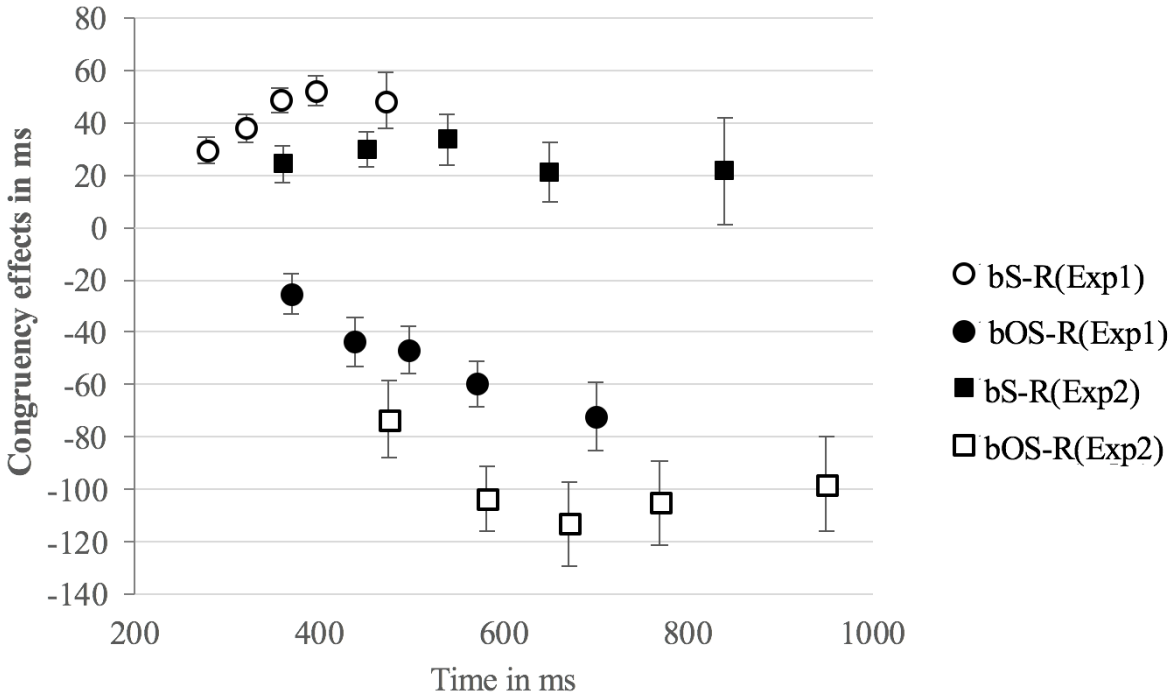


Figure 10: Shows the SCy and R-SCy effects in ms (y-axis) over RT-length (x-axis) from Experiment 1 (18 participants) and 2. In Experiment 1, the SCy effect and its reversal increased with increasing RT. In Experiment 2, a significant quadratic effect was observed in the bOS-R task. This indicated that the R-SCy effect increased with increasing RT but decreased again after the third quintile.

Response accuracy distribution bS-R task for 18 participants: RM ANOVA showed a main effect of spatial CONGRUENCY, $F(1,17)=25.57$, $p<0.001$, $\eta^2=0.60$, a main effect of QUINTILE, $F(2,41) =5.29$, $p<0.01$, $\eta^2=0.24$ (GG), and a significant inter-

action F(4,68)=10.95, p<0.001, η^2=0.39 (Figure 11). Post hoc tests indicated a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=8.6% , Std error = 1.972, p<0.001), second (MD=8.5 % , Std error = 1.408, p<0.001) and third (MD=2 % , Std error = 0.944, p<0.05) quintile. On all three occasions, participants made more errors on spatially-incongruent in comparison to spatially-congruent trials. In addition, a linear effect was found in the spatially-congruent (F(1,17) = 8.16, p < 0.05), and spatially-incongruent (F(1,17) = 19.28 , p < 0.001) conditions. Whereas the former showed more errors for slow responses the latter revealed more errors for fast responses (Figure 11).

bOS-R task: RM ANOVA showed a main effect of spatial CONGRUENCY, F(1,17) = 22.99, p < 0.001, η^2=0.58, a borderline effect of QUINITLE, F(4,68) =2.49, p=0.051, η^2=0.13, and a significant interaction F(2,39)=7.39, p=0.001, η^2=0.30 (GG; Figure 11). Post hoc tests indicated a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=12.3 % , Std error = 3.572, p=0.003), second (MD=14.2 % , Std error = 3.023, p<0.001) and third (MD=12.3 % , Std error = 2.271, p<0.001) quintile. On all three occasions, participants made more errors on spatially-congruent in comparison to spatially-incongruent trials. In addition a linear effect was found in the spatially-congruent condition, F(1,17)=11.30, p<0.01, and a borderline effect was revealed in the spatially-incongruent condition ,F(1,17) = 3.94 , p < 0.06. The former showed more errors for fast responses whereas the latter revealed the opposite tendency (Figure 11).

Standard deviation analysis for 18 participants: RM ANOVA with TASK and spatial CONGRUENCY as factors revealed a significant main effect of TASK F(1,17)=39.59, p<0.001, η^2=0.70, a main effect of spatial CONGRUENCY, F(1,17)= 6.48 , p<0.05, η^2=0.28, and a significant interaction, F(1,17)=17.33, p < 0.01, η^2=0.51. Post hoc test indicated that the standard deviation in the bS-R task was significantly smaller than in the bOS-R task (MD=57.4, Std error =9.1, p<0.001) and that the spatially-congruent

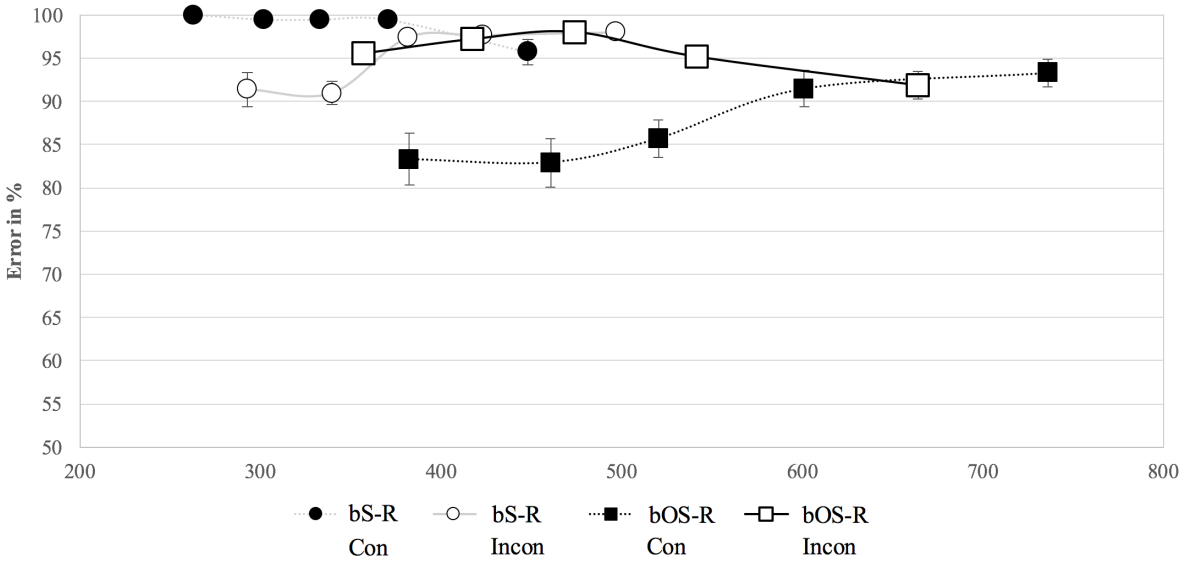


Figure 11: Shows the response accuracy in percentage (y-axis) over RT-length in ms (x-axis) from Experiment 1 for 18 participants. In the bS-R task more fast errors were made in the spatially-incongruent in comparison to spatially-congruent condition. This was reversed in the bOS-R task.

condition overall revealed a larger standard deviation than the spatially-incongruent condition (MD=9.5, Std error =3.7, $p<0.05$). Further, the standard deviation in the bOS-R task was larger in the spatially-congruent in comparison to spatially-incongruent condition (MD=23.3 , Std error=5.2, $p<0.001$). No difference between the standard deviation of spatially-congruent and spatially-incongruent trials was found in the bS-R task (MD=4.3, Std error = 4.7, $p>0.05$; Figure 8).

The results for 20 and 18 participants were strikingly similar, although two participants acted very different from the rest of the group. This shows that the remaining 18 participants had a very consistent behavior. The notable difference in the results occurred in the reaction time distribution. Whereas the SCy effects in the bS-R task increased with increasing RT for 18 participants, this effect was not significant for 20 participants. Although, a strengthening of the SCy effect is observed until the fourth quintile, the large variance in quintile 5 likely causes this null finding. Hence, it is likely that the increasing trend of the SCy effect in the bS-R task is an actual phenomenon. Therefore, the results from 18 participants will be the focus of the upcoming discussion.

2.4 Discussion – Experiment 1

Experiment 1 was set-up to assess the SCy and R-SCy effects to understand which processes (automatic vs. deliberate) carry these effects. Understanding how generic S-R mappings function is important when examining the unique role of biological S-R contingencies. Therefore, the study of Boyer et al. (2012) was replicated using a within-subject design while putting high priority on the accuracy of the experimental equipment (See Introduction - Experiment 1 and 2 for more detail). The aim was to replicate the findings of Boyer et al. (2012) that deliberate processes influence long-term spatial S-R mappings in the bOS-R task. Such findings could support the conclusion that spatial stimuli do not always trigger the associated (matching) action, which dissociates the processing of spatial and biological cues.

A SCy effect was revealed in the bS-R task whereas a R-SCy effect was shown in the bOS-R task. Both effects were approximately 10-20 ms larger than the effects seen in the study of Boyer et al. (2012). In general, this pattern of SCy and R-SCy effects indicate that the processing of task-irrelevant spatial stimuli is influenced by task instructions (Hedge & Marsh, 1975).

2.4.1 The Processes underlying SCy and R-SCy effects - RTs over time

Interestingly, the SCy and R-SCy effects increased with increasing RTs as was observed in the study of Boyer et al. (2012). This is important since the median RTs in the current experiment was between 60 and 80 ms faster than the RTs in the experiment of Boyer et al. (2012) [14]. The (absolute) magnitude of the SCy and R-SCy effects in the first quintile was larger than 20 ms, whereas these effects were considerable smaller or nonexistence in the study of Boyer et al. (2012).

Usually, the SCy effect in S-R tasks becomes smaller with increasing RT, since the deliberate pathway inhibits the automatic congruent response (Proctor et al., 2011). Wiegand and Washer (2005) suggested that an increasing SCy effect with increasing time occur

[14] This could result from Boyer et al. (2012) using mean RTs instead of median RTs.

when a cognitive Simon effect is elicited in comparison to a visuomotor Simon effect. The visuomotor Simon effect is characterized by the connection between the hemisphere activated by the perceived stimulus and the hemisphere used for responding. For example, in of the original experiments, Simon et al. (1970) presented a stimulus to the right or the left side and let participants respond with the right or the left hand. On spatially-congruent trials, the same hemisphere was activated when observing the stimulus and executing the response. This triggered a visuomotor Simon effect, which strongly relied on the learned long-term S-R mechanisms. In contrast, the cognitive Simon effect was elicited when a unimanual paradigm or centrally presented task-irrelevant stimuli (e.g. arrows or directional words) were used. In such cases, the participants needed to interpret the task-irrelevant stimulus and could not rely on the built-in hemispheric connectivity. Interpretation of the task-irrelevant stimulus took time, and therefore the cognitive Simon effect increased with increasing RT. This theory was supported by different studies showing that cognitive Simon effects showed increasing delta plot slopes (Ansorge, 2003; Wiegand & Wascher, 2007; Pellicano, Lugli, Baroni, & Nicoletti, 2009). However, Wiegand and Wascher (2007) disproved this theory when using a unimanual mixed-trial paradigm and revealing a decreasing slope in a delta plot. According to their theory, all unimanual experiments should elicit cognitive Simon effects, which gradually increase. Further, Catmur et al. (2011) also used a unimanual S-R paradigm and found no effect of response time on the size of the SCy effect. Lastly, auditory Simon tasks, in which tones are played into the right or the left ear (task-irrelevant stimulus) and the participants make a left/right response based on the pitch of the tone (imperative stimulus) consistently show increasing slopes in delta plots. According to Wiegand and Wascher (2005), such auditory Simon tasks should show a decreasing slope, since the same hemisphere primarily processes the tone and executes the response. From these studies, it is difficult to determine why Experiment 1 revealed an increasing SCy effect in the bS-R task with increasing time.

In contrast to the delta plot in the bS-R task, the increasing R-SCy effect in the

bOS-R task was in line with the results of Dejong (1994) described in the Introduction to Experiment 1 and 2. According to the action-suppression model, this suggests that deliberate processes influenced the automatic and spatially-congruent responses gradually and thereby increased the R-SCy effect with increasing time (Ridderinkhof, 2002). However, the analysis of the variances between the spatially-congruent and spatially-incongruent conditions also revealed a significant difference [15], which predicted a negative slope (Proctor et al., 2011). Hence, it is likely that the differences in variances between conditions contributed to the observed pattern of the delta plot.

2.4.2 The processes underlying SCy and R-SCy effects - Response accuracy over time

In the bS-R and bOS-R tasks the pattern of the fast errors resembled the respective congruency effects. In the bS-R task, more fast errors were seen in the spatially-incongruent condition. This was reversed in the bOS-R task, indicating that fast responses were in favour of the spatially-incongruent response. If automatic long-term S-R associations guided responding, a fast tendency to respond in congruence with the task-irrelevant spatial stimulus should have emerged in both tasks. According to the action-suppression model described in the Introduction to Experiment 1 and 2, these results show that spatial S-R mappings are influenced by deliberate processes, promoting the task-defined mapping rule, before participants can respond.

All in all, the effects in the present study resembled the results from Boyer et al. (2012), which shows the reliability of spatial S-R contingencies. Since the present study used a within-subject design, whereas Boyer et al. (2012) employed a between-subject design, one can conclude that inter-sample variance did not affect the SCy and R-SCy effects in their study. Further, the results support that single-route and direct-matching models of Sauser and Billard (2006), which simulate how deliberate top-down processes control spatial S-R mapping.

[15] Increased variance in the spatially-congruent in comparison to spatially-incongruent condition.

2.4.3 Aims of Experiment 2

In Experiment 2, a mixed design is used to test whether response strategies mediated the results observed in Experiment 1. Blocked experimental designs can allow the formation of response strategies (e.g. blurring the vision, focusing on specific parts of the image) by repeating the same task continuously (Catmur & Heyes, 2011). Experiment 2 uses a pre-cue at the beginning of each trial, which indicates whether participants need to perform a bS-R task or a bOS-R task. Else Experiment 2 is identical to Experiment 1. A SCy effect in the bS-R task and R-SCy effect in the bOS-R task are expected. Based on the results found in Experiment 1, an immediate influence of short-term S-R mechanisms on long-term S-R associations should be observed in the bOS-R task. That is, the R-SCy effect should appear from the fastest to the slowest RTs, and more fast errors should occur in the spatially-congruent in comparison to spatially-incongruent condition. Mixed paradigms add additional mental processes (e.g. increased working memory load), which could increase the variance in the data (Proctor & Fisicaro, 1977; Los, 1996). Since delta plots are affected by the observed variance within the congruent and incongruent conditions, the plots in Experiment 2 could show variations from the results in Experiment 1 (J. Zhang & Kornblum, 1997).

2.5 Methods – Experiment 2

2.5.1 Participants

Twenty-six right-handed volunteers participated in this experiment. Three participants were excluded from the analysis (two due to equipment error, one who made more than the allowed numbers of errors). Thus, 23 participants (mean age = 25.5, sd = 2.4 , females = 14) were included into the analysis. On average 12 percent of the trials were removed from the analysis. Informed written consent was received before participation, and the study was approved by the STEM ethics committee at the University of Birmingham.

2.5.2 Experimental design and analysis

Coloured frames were presented at the beginning of each trial indicating whether to respond following the bS-R or the bOS-R task. RTs below 200 ms and above 1500 ms were categorized as outliers and not included in the analysis. The cut-off of 1500 ms was chosen to be higher than the cut-off used in the experiment of Boyer et al. (2012) to account for the increased task difficulty. Else the experiment was similar to Experiment 1 (Figure 12).

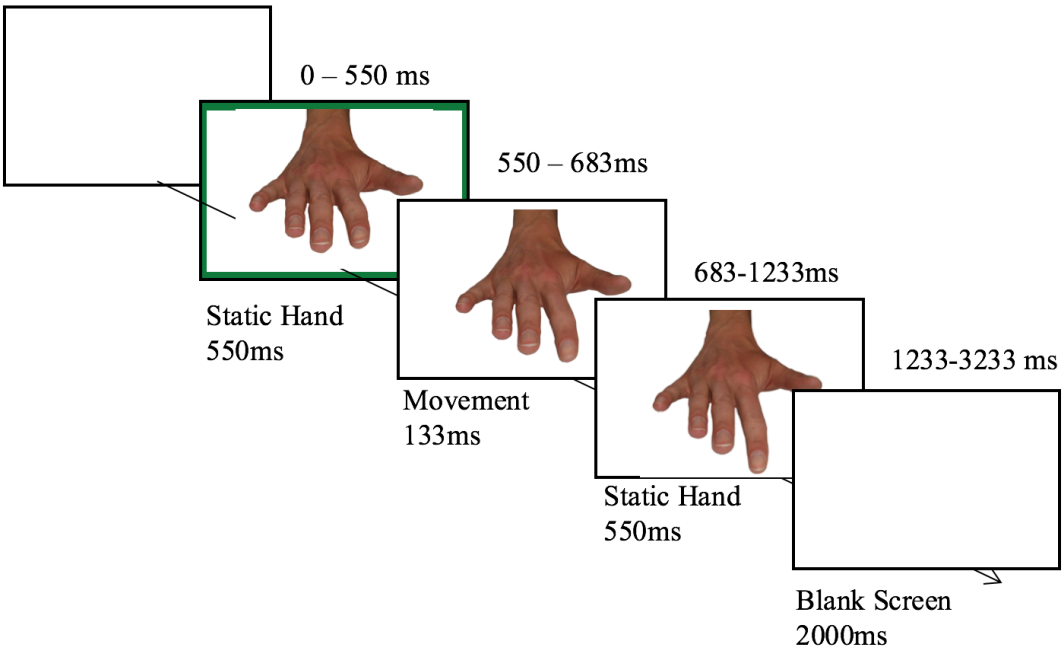


Figure 12: The time line of Experiment 2 (as well as Experiment 4 in Chapter 3). A trial began with a blank screen (2000 ms). Then the stationary hand in a neutral position was shown (550 ms) simultaneously a coloured frame (green or red) appeared, which indicated which task (bS-R vs bOS-R) to perform. Next, 8 successive frames (133 ms) created the impression of a tapping movement of the index or middle finger. Lastly, a static hand in the end position was shown (550 ms). Participants could respond as soon as the hand on the screen started moving (0 ms).

2.6 Results – Experiment 2

Congruency effects: RM ANOVA revealed a main effect of TASK on response times, $F(1,22) = 170.09$, $p < 0.001$, $\eta^2 = 0.89$, indicating that participants responded faster in the

bS-R task in comparison with the bOS-R task (MD=132.1, Std error=10.1, p<0.001). Also, a significant effect of spatial CONGRUENCY was revealed, F(1,22)=13.17, p<0.001, η^2=0.37, indicating that participants responded faster in the spatially-incongruent condition (MD=39.9 ms, Std error=11, p<0.01). A significant interaction between TASK and spatial CONGRUENCY, F(1,22)=92.15, p<0.001, η^2=0.81, and follow-up post hoc comparisons revealed that responses were faster during spatially-congruent trials in comparison to spatially-incongruent trials in the bS-R task (MD=33.0 ms, Std error = 9.8, p,< 0.01), whereas participants were faster during spatially-incongruent trials in the bOS-R task (MD=112,9 ms, Std error = 16.2, p<0.001; Figure 13A)

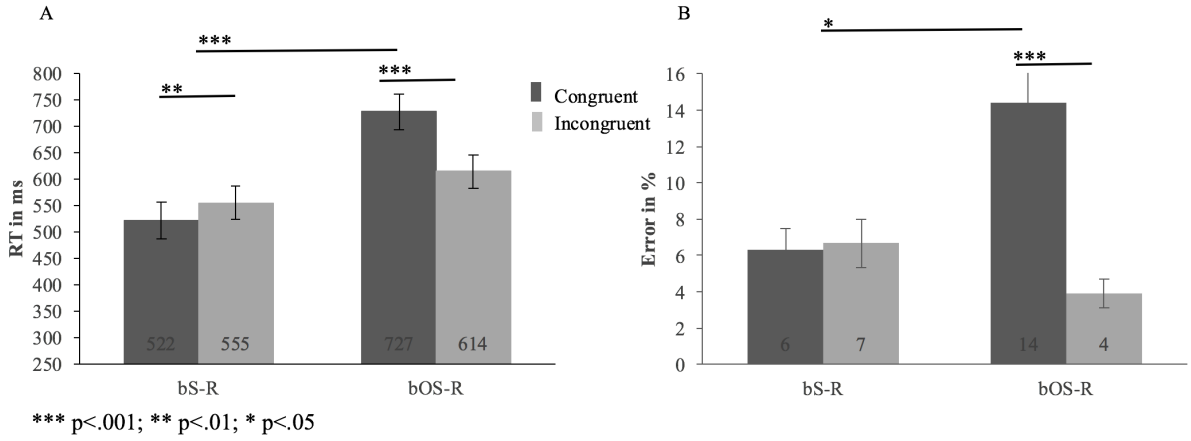


Figure 13: Shows the (A) RTs and (B) error rates in the bS-R and bOS-R tasks of Experiment 2. In the bS-R task RTs were faster in the spatially-congruent condition than in the spatially-incongruent condition. This was reversed in the bOS-R task. In the bOS-R task error rates were lowest in the spatially-incongruent condition in comparison to spatially-congruent condition. No significant difference was found in the bS-R task.

Error rate analysis: RM ANOVA with TASK and spatial CONGRUENCY as factors showed a significant main effect of TASK, F(1,22)=5.45, p<0.05, η^2=0.20, indicating that participants made more errors in the bOS-R task (MD=2.6 %, Std error=1.1, p<0.05). A significant main effect of spatial CONGRUENCY, F(1,22)=25.84, p<0.001, η^2=0.54, showed that participant made more errors in the spatially-incongruent condition (MD=5.4 %, Std error=1.1, p<0.001). A significant interaction, F(1,22)=35.12 p<0.001, η^2=0.62, and post hoc tests showed that participants made significantly more errors in the spatially-

congruent condition compared to the spatially-incongruent condition in the bOS-R task (MD=-10.5 %, Std error = 1.7, p<0.001). No difference was found in the bS-R task (MD=0.3 %, Std error = 0.9, p>0.05; Figure 13B).

Reaction time distribution: RM ANOVA showed a significant main effect of TASK, F(1,22)=62.94 , p < 0.001, η^2=0.74, but no interaction between TASK and QUINTILE, F(2,42)=2.22, p>0.05, η^2=0.09 (GG). No linear effect was found in the bS-R, F(1,22)=0.08, p>0.05, or bOS-R tasks, F(1,22)=1,26, p>0.05. However, a significant quadratic effect was found in the bOS-R task, F(1,22)=6.12, p < 0.05, indicating that the R-SCy effect initially increased with increasing response times (until the third quintile) before slightly decreasing in quintiles 4 and 5; Figure 10)

Response accuracy distribution bS-R task: RM ANOVA showed a main effect of QUINTILE, F(1,26) = 19.58 , p<0.001, η^2=0.47 (GG), and a significant interaction between QUINTILE and spatial CONGRUENCY, F(1,29)=4.68, p<0.05, η^2=0.18 (Figure 14). Post hoc tests revealed a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=1.7 % , Std error = 0.69, p<0.05) , third (MD=2.5 % , Std error = 0.87, p<0.05) and the fifth (MD= 11.8 % , Std error = 5.67, p<0.05) quintile. This showed that the spatially-incongruent condition triggered more errors than the spatially-congruent condition when responses were fast. This effect got reversed for quintile three and five. Hence, on slower trials, more errors were made in the spatially-congruent condition (Figure 14). Besides, a linear effect was found in the spatially-congruent condition, indicating that more errors were made with longer RTs, F(1,22)=14.54, p=0.01. No linear effect was found for the spatially-incongruent condition, F(1,22)=0.87, p=0.362.

bOS-R task: RM ANOVA showed a main effect QUINTILE, F(1,32) = 6.36 , p<0.001, η^2=0.22 (GG), and a significant interaction between QUINTILE and spatial CONGRUENCY, F(2,42)=4.48, p<0.05 η^2=0.17 (GG). Post hoc tests revealed a significant difference in response accuracy between spatially-congruent and spatially-incongruent trials in the first (MD=11.2 % , Std error = 0.69, p<0.01), second (MD=8.2 % , Std error = 2.14,

$p<0.01$) third (MD=3.9 % , Std error = 1.49, $p<0.05$) and the fifth (MD= 15.1 % , Std error = 4.52, $p<0.01$) quintile (Figure 14). For all quintiles more errors were made in the spatially-congruent in comparison to spatially-incongruent condition. Additionally a linear effect was found for the spatially-congruent, $F(1,22)=7.95$, $p<0.001$, and spatially-incongruent, $F(1,22)=8.03$, $p<0.05$, conditions. In both cases, more errors were observed with faster responses. However as seen in Figure 14, the effect was more pronounced in the bOS-R task.

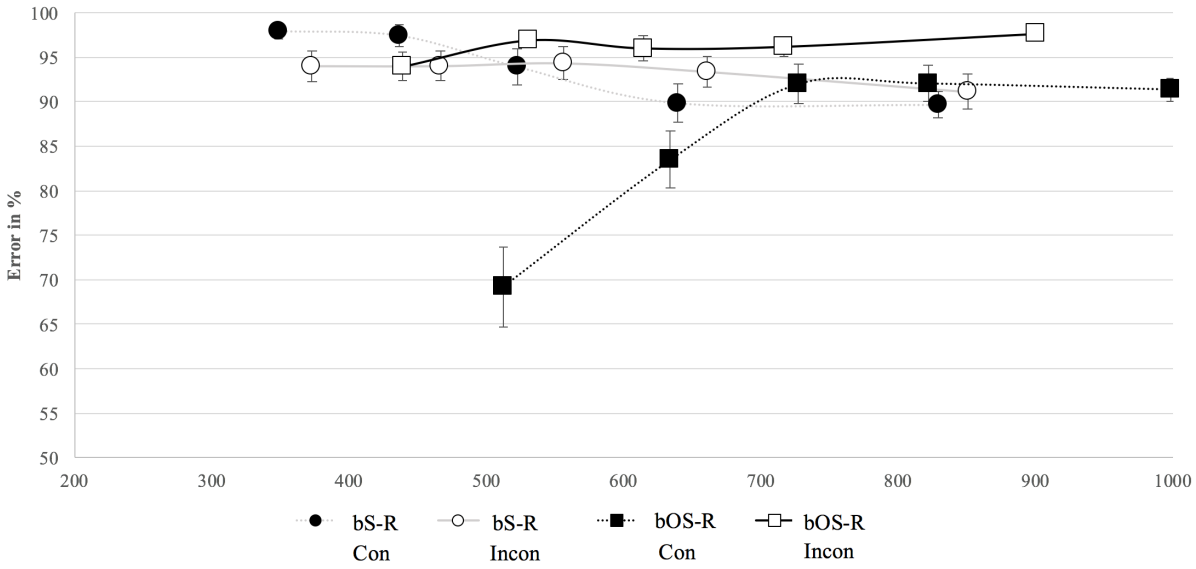


Figure 14: Shows the response accuracy in percentage (y-axis) over RT-length in ms (x-axis) from Experiment 2. In the bS-R task more fast errors were made in the spatially-incongruent in comparison to spatially-congruent condition. This was reversed in the bOS-R task.

Standard deviation for each condition: RM ANOVA with TASK and spatial CONGRUENCY as factors revealed no significant main effect of TASK, $F(1,22)=1.21$, $p>0.05$, $\eta^2=0.052$, no main effect of spatial CONGRUENCY, $F(1,22)= 1.454$, $\eta^2=0.06$, and no significant interaction, $F(1,22)=0.014$, $p > 0.05$, $\eta^2=0.00$, (Figure 8).

2.7 Discussion – Experiment 2

2.7.1 SCy and R-SCy effects

The present experiment was set-up to assess the SCy and R-SCy effects using biological imperative stimuli in a mixed within-subject design (See Introduction - Experiment 1 and 2 for more details). The RTs increased by approximately 100 ms in Experiment 2 in comparison to Experiment 1, but both experiments revealed SCy and R-SCy effects. This replicates the main effects from Boyer et al. (2012) as well as the results found in the study of Boyer, Scheutz and Bertenthal (2009), which both used the same paradigm as the current study. It shows that the Simon effect as well as its reversal are very stable phenomena.

What do these effects suggest regarding the processing of spatial stimuli? As pointed out in the General Introduction, the ideomotor theory suggests that SCy effects are guided by long-term S-R associations, which are learned by repeated exposure. The more often a sensory stimulus is coupled with the same action, the stronger is the association between sensory information and the executed movement. Therefore, perceiving similar sensory events can trigger a related movement. The theory suggests that people are reacting in a compatible manner throughout there lives: For example, when a person grasps an object on the right side, it is coupled with a shift in attention to the right (Galletti et al., 2010). When the connection between right-sided attention and right-sided grasp has been learned, a spatial stimulus appearing in the right hemifield captures the attention of the observer and promotes a movement to the right and not to the left side. In contrast, to the SCy effect, its reversal in the bOS-R task is influenced by short-term S-R associations, which are processed more deliberately (De Jong et al., 1994). According

to the action-suppression model (See, Introduction - Experiment 1 and 2), the deliberate processes, which are based on S-R associations determined by the task instructions, can control the automatic congruent response (Ridderinkhof, 2002). By means of logical recoding, the deliberate route influences the S-R mapping of the task-relevant and irrelevant stimuli so that they fit the requirements of the task instructions. Therefore, the spatially-incongruent response is faster and less error prone than the spatially-congruent response in the bOS-R task.

2.7.2 The processes underlying SCy and R-SCy effects - RTs over time

A distributional analysis (Ratcliff, 1979) was used to give more insights into the cognitive processes underlying the SCy and R-SCy effects (Proctor et al., 2011). Specifically, the slopes of the resulting delta plots, which show whether a congruency effect decreases or increases with time, reveals if the congruency effect was triggered by short-term or long-term S-R associations (Dejong 1994). However, evidence exists, which shows that the slopes of delta plots depend on the variance of the RTs within the spatially-congruent and spatially-incongruent conditions. When the variance is higher in the spatially-incongruent than in the spatially-congruent condition, the slope is negative and vice versa (J. Zhang & Kornblum, 1997). Therefore, the current study included statistical testing of the variances between conditions. For most tasks, there was no significant difference between variances in the spatially-congruent and spatially-incongruent conditions. Only the bOS-R task in Experiment 1 revealed increased variance in the spatially-congruent in comparison to spatially-incongruent condition. According to Zhang and Kornblum (1997), this should lead to a negative slope, which was indeed observed in this specific situation.

Across quintiles the SCy effects were greater in Experiment 1 than in Experiment 2. In contrast, the R-SCy effects were always greater in Experiment 2 in comparison to Experiment 1. The latter finding was quite remarkable since, the R-SCy effect in Experiment 2 ranged up to 110 ms in the third quintile and hence, was much larger than what has been reported using a similar paradigm (Bertenthal et al., 2006; Boyer et al.,

2012). This might show that the increase in cognitive control used during task-switching in the mixed task (Proctor & Fisicaro, 1977), increases the R-SCy effect since this effect draws on the same deliberate processes.

In Experiment 1 the SCy and R-SCy effects increased with increasing RT. In Experiment 2 there was no significant effect of response time on the SCy effect. In contrast, the R-SCy effects increased until approximately 680 ms (third quintile). This was followed by a slight decrease (from -110 ms to -100 ms) until the last quintile.

Dejong (1994) published the only study, in which S-R and OS-R tasks were mixed within the same experimental block. In the blocked and mixed experiments, the SCy effects in the S-R task decreased with increasing RTs, and the R-SCy effects in the OS-R task increased with increasing RTs. However, other studies have shown that adding a discriminative stimulus, as the coloured frame in Experiment 2, can alter the slope of the resulting delta plots. For example, in the experiment of Wiegand and Wascher (2007) participants perform a fixed Simon-like experiment as well as mixed experiment, where they included a discrimination task. In both experiments, participants reacted to the letters 'A' and 'B' presented on the left or right side of the screen with a button press to the right or left side. In the fixed task, a letter 'A' was associated with a left button press, and a letter 'B' was associated with a right button-press. In the mixed experiment, the mapping rule depended on the discriminative stimulus (a circle or square appearing in the centre of the screen). A circle prompted the participants to press the left key when an 'A' appeared and the right key when a 'B' appeared (This was reversed when a square appeared). Therefore, participants depended their S-R mapping on the discriminative stimulus as participants depended their mapping rule (bS-R vs bOS-R) on the coloured frame in Experiment 2. In Wiegand and Wascher's (2007) experiment, the fixed task showed an increasing slope in the delta plot, whereas the mixed task revealed a decreasing slope. Hence, the mixed design significantly changed the slope of the delta plot as has been seen in the present studies. Why this occurs is not yet understood. However, it is likely that the increased cognitive control required in the mixed task strengthens the

deliberate route of the action-suppression model and thereby influences the automatic long-term S-R associations throughout the experiment (Proctor & Fisicaro, 1977; Los, 1996; R. K. Ridderinkhof, 2002). Ridderinkhof (2002), termed such global strengthening of the deliberate route based on task characteristics macro-adjustments and he added that these adjustments influenced performance more than micro adjustments, which are formed on a trial-by-trial basis.

Importantly, Bertenthal et al., (2006) also used the same design as the present study and the temporal dynamic of the SCy effect in the S-R task was also assessed. They found no significant effect of RT-length on the magnitude of the SCy effect. In other words, they found the same result as in Experiment 2. Their result directly contradicts the later findings of Bertenthal's research group, showing an increasing SCy effect with increasing time (Boyer et al., 2012). This indicates that delta plots in bS-R tasks are very variable and that more research is required to understand what influences its slope. However, an important insight is that none of the studies using the present paradigm (including the present study) found a decreasing SCy effect with increasing time. As described in the Discussion of Experiment 1, this could be due to the unimanual paradigm, which triggered a cognitive Simon effect (Wascher and Wiegand, 2005; Wascher and Wiegand, 2007a).

In contrast to the delta plots in the bS-R tasks, there is only a slight discrepancy between the delta plots in the bOS-R tasks of Experiment 1 and 2. Both experiments show that the R-SCy effect increases with slower responses [16]. Secondly, both experiments reveal a R-SCy effects from the fastest RTs on-wards. Dejong (1994) also found an increasing R-SCy effect with increasing time. According to the action-suppression model, this shows that deliberate processes, which build-up with time, gradually suppresses the automatic congruent response. Since the R-SCy effect was found for the fastest RTs onwards, the deliberate mechanisms were stronger than the automatic processes before participants began responding. Experiment 3 and 4 will examine whether the processing of biological stimuli is influenced alike.

[16] Although a slight trend in the opposite direction is observed for the last quintiles in Experiment 2.

2.7.3 The processes underlying SCy and R-SCy effects - Response accuracy over Time

Assessing the response accuracy over time supported the insights about the interaction between automatic and deliberate processes in the bS-R and bOS-R tasks. In accordance with the dimensional overlap-and the active-suppression model, the fastest responses should be more influenced by the automatic than the deliberate route, since the former is activated immediately, whereas the latter is activated slower. Hence, the fastest errors in the bS-R and bOS-R tasks should be in accordance with the learned S-R mapping, which is the spatially-congruent response. However, in both experiments, the fastest errors resembled the pattern of the congruency effects. That is, in the bS-R task more fast errors occurred in the spatially-congruent condition. This pattern was reversed in the bOS-R task. Here the spatially-incongruent response was favoured since most fast errors occurred in the spatially-congruent condition. These results clearly show that short-term S-R mechanisms influence the processing of spatial stimuli in the bOS-R task before participants can respond, which also is proposed by the computational models of Sauser and Billard (2006).

As described in the General Introduction, both models suggest that spatial cues are first processed in retinal coordinates and transformed into spatial coordinates in the medial STS located in the 'where stream'. Within this stream, the visual-spatial information is processed in the PPC, where the S-R mapping occurs (Andersen, Snyder, Bradley, & Xing, 1997). The PFC acts as a moderator during this last step. It incorporates task rules into the S-R mapping process.

The present results, as well as the single-route and direct-matching models, do not claim that the long-term S-R associations are not relevant at all. Past work has consistently revealed one feature, which stresses the importance of learned S-R mappings: In general, people respond faster in S-R tasks, where learned S-R associations are consciously used, than in OS-R tasks, setting aside the nature of the imperative stimulus (Hasbroucq & Guiard, 1991; Hedge & Marsh, 1975; Proctor & Pick, 2003). In Experiment 1 and 2,

faster RTs were also found in the S-R task in comparison to the OS-R task, and the variability in the data explained by this difference was higher than the variability in the data explained by the congruency effects. This topic will be discussed further in Chapter 3.

3 Chapter 3

3.1 Introduction – Experiment 3 and 4

In the previous study, SCy effects were assessed using imperative biological stimuli. This was done to understand the cognitive processes underlying generic S-R contingencies, which later are compared to the cognitive mechanisms involved in automatic imitation. In the present chapter the experiments from Chapter 2 will be repeated, but instead of measuring SCy effects, BCy effects will be assessed. With the results from both chapters, it is possible to conclude whether BCy and SCy effects provide enough behavioural evidence to determine if the stimuli are processed differently.

With the discovery of mirror neurons, research has accumulated, which suggests that humans have developed a particular neural circuit to process biological stimuli (Iacoboni, 2005). This neural circuit is proposed to facilitate imitation and to interfere with behaviour if imitation is not required. The results from Experiment 1 and 2 suggested that spatial S-R mappings are controlled by deliberate processes, which take the task rules into account. To date, there is convincing evidence that biological cues are not influenced by such deliberate processes (Bertenthal et al., 2006; Boyer et al., 2012). In the General Introduction automatic imitation was already introduced. The upcoming paragraphs will provide additional information to get a better understanding of automatic imitation and to become familiar with the evidence pointing towards the unique S-R mapping mechanisms for biological stimuli.

3.1.1 Paradigms measuring the automatic Imitation effects

As described in the General Introduction, automatic imitation was first studied by, Brass et al., (2000), who used an S-R task to distinguish between the influence of biological (finger tap) and spatial cues (cross superimposed on the hand) on response times. A SCy and a BCy effect was elicited but the latter was considerable larger, which supported the conclusion that the observation of biological stimuli promotes matching actions more than

the observation of spatial stimuli.

In a follow up study Brass, Bekkering and Prinz (2001) assessed whether the increase of biological-feature overlap between the observed stimulus and the executed response increased the influence of long-term S-R associations on behavior. In the first experiment, a hand was presented on the screen, which could either tap or lift the middle or index finger. Depending on the experimental block participants responded with an index finger lift or tap. It was of interest to assess whether the match between stimulus and effector identity (finger type) or the match between stimulus and finger movement (lift or tap) was crucial for automatic imitation. In a second experiment, the task remained the same, but instead of a hand, a non-biological stimulus was used to determine whether it would trigger similar behavioural effects as the biological cue. Lastly, experiment one was repeated with the distinction that the hand was flipped up-side-down or kept in the third person perspective depending on the experimental block. This was done to compare the effects of biological identity (middle or index finger) and movement trajectory (on upward or downward movement) on response speed. The experiments revealed congruency effects for biological (hand) and non-biological cues. However, the BCy effect was significantly larger than the SCy effects. Lastly, the biological nature of the stimuli influenced RTs more than the movement trajectory of the stimulus, although both manipulations triggered an automatic imitation effect. These results led to the conclusion that BCy and SCy effects use similar but not identical cognitive mechanisms. Since the effects of biological cues were more pronounced, it was proposed that biological stimuli are processed more automatically than spatial stimuli and directly mapped onto the observer's motor system.

3.1.2 Limitations of automatic imitation studies

Many of the studies exploring automatic imitation with S-R paradigms shared similar limitations in the experimental design (Stürmer, Aschersleben, & Prinz, 2000; Brass et al., 2000, 2001; Gowen et al., 2010). For example, the task-irrelevant biological stimulus used by Brass et al. (2000) also included spatial properties as both the observed finger

movements and the participant's responses always occurred left- or right-of-centre. Thus, it is not actually possible to make conclusive interpretations about whether the automatic imitation effects were over and above those generated by Simon-like effects. A second criticism is that automatic imitation studies have not always controlled for stimulus saliency (Jansson et al., 2007). To test whether the BCy effects were different from non-BCy effects, Jansson et al. (2007) compared RTs to biological and non-biological cues, which were matched in saliency and did not match-up spatial and biological features. In general, RTs were faster, if the cue and the response were congruent in comparison to incongruent, but there was no difference in effect magnitude between the effects triggered by biological and non-biological cues. They reasoned that stimulus salience rather than its biological nature mediated the effects of prior studies reporting a more pronounced BCy in comparison to SCy effect (Brass et al., 2001; Press et al., 2005; Kilner et al., 2003). This raises the question whether automatic imitation is a form of S-R compatibility, which does not depend on the existence of a specialized neural pathway dedicated to matching the observed action onto the observer's body. Thus, biological cues would not be processed differently than other visual cues (Catmur & Heyes, 2011; Cooper, Catmur, & Heyes, 2013).

Using an S-R task but controlling for saliency differences and confounding variables, Bertenthal et al. (2006) were the first to use the present paradigm to elicit SCy and BCy effects (See, Introduction - Experiment 1 and 2). Bertenthal et al. (2006) reported the presence of both automatic imitation and spatial cueing effects. However, the latter was significantly more pronounced. Hence, the results contradicted findings, revealing greater BCy in comparison to SCy effects (Brass et al., 2001; Newman-Norlund, 2010). Delta plots revealed that the SCy effect remained stable over time, whereas the BCy effect was present for fast RTs and disappeared afterwards. The authors interpreted these results according to the action-suppression model (See, Introduction - Experiment 1 and 2). They reasoned that the BCy effect was induced by activity in an automatic pathway using long-term S-R associations, which was inhibited over time by activity in the deliberate pathway using short-term S-R associations. In contrast, the influence of task-irrelevant spatial stimuli

was not inhibited similarly. Instead, short-term S-R associations might have contributed to the SCy effect. This, in turn, would support the idea that automatic imitation and automatic spatial S-R mappings rely on different cognitive mechanisms.

3.1.3 Is automatic imitation based on long-term S-R association

In recent years a contrasting view has developed, which suggests that SCy and BCy effects are based on associative learning. For example, Press et al. (2005) examined whether robotic and human stimuli generate automatic imitation effects. Participants saw a human or a robotic representation of a hand, which performed an opening or closing movement. Depending on the experimental block participants were told to perform an opening or closing movement with the hand whenever they observed the stimulus on the screen. It was of interest to examine RTs when the stimulus movement and the response was compatible in contrast to incompatible. Results indicated that robotic and human stimuli elicited compatibility effects (faster RTs when the movements were the same as compared to the opposite). Importantly, this effect was stronger for human than for robotic stimuli. The results were interpreted in line with the associative learning theory, which describes that automatic imitation is a learned behaviour and increases with increasing experience. Further, the automatic imitation effect depends on the resemblance between the stimulus in the experiment and the stimuli encountered by experience. If the similarity between the stimuli increases so does the automatic imitation effect. The more pronounced automatic imitation for human stimuli in comparison to robotic stimuli was therefore explained by the higher resemblance between the experimental stimulus and real-life encounters.

Interestingly, the difference in magnitude between human and robotic compatibility effects was abolished if participants received training to react to robotic stimuli beforehand (Press, Gillmeister and Heyes, 2007). This shows that increasing experience with S-R mappings strengthens their influence on behavior and therefore it is likely that biological S-R mappings are acquired similarly.

Lastly, Catmur and Heyes (2011) argued that differences between SCy and BCy effects

could be attributed to the increased complexity of biological in comparison to spatial stimuli, which meant that biological stimuli needed more time to be processed. Hence, the effects of biological stimuli increased with time, whereas the SCy effect often decreased with increasing RT (Brass et al., 2001).

All in all, using S-R paradigms to compare spatial and biological cueing did not give definite answers about the similarity of the underlying processes, since spatial and biological task-irrelevant cues elicited a congruency effect. However, with the discovery of the R-SCy effects, the processing of spatial and biological stimuli could be compared in an additional paradigm.

3.1.4 Using OS-R tasks when comparing spatial and biological S-R Mappings

The importance of the OS-R task in assessing automatic imitation was highlighted in the General Introduction and in Chapter 2. There the direct-matching and the single-route models illustrated that biological task-irrelevant stimuli do not elicit a R-BCy effect if task-irrelevant biological stimuli are mapped directly onto the observer's motor system according to the mirror neuron account. However, if biological stimuli are processed similarly to task-irrelevant spatial stimuli, they should also evoke a R-BCy effect in the OS-R task (Sauser and Billard, 2006). As described in Chapter 1 and 2 , Boyer et al. (2012) set-up a behavioural paradigm to test these assumptions and since they found a R-SCy effect but not a R-BCy effect, they concluded that logical recoding does not influence the processing of biological stimuli. Instead, biological stimuli are directly mirrored onto the observer's motor system, which always promotes imitation.

Experiment 1 and 2, replicated the bS-R and bOS-R tasks of Boyer et al. (2012) and found the same results for task-irrelevant spatial stimuli: A SCy effect in the bS-R task and a R-SCy effect in the bOS-R task. This showed that slow and deliberate processes influenced the S-R mapping of task-irrelevant spatial. This interpretation was strengthened by the finding that fast errors in the bOS-R task occurred in favour of the spatially-incongruent response. Hence, even the fastest responses in the bOS-R task were

subject to logical recoding, which strongly suggested that automatic congruent responses were immediately controlled by more deliberate processes.

3.1.5 Aim of the current study

After having established which behavioural effects are induced during non-biological S-R mapping, Experiment 3 is set-up to assess the potential unique S-R mechanism of task-irrelevant biological cues. It is of particular interest to investigate whether task-irrelevant biological stimuli show a R-BCy effect in the sOS-R task and therefore are processed in a single-route together with spatial stimuli. To do this the sS-R and sOS-R tasks from Boyer et al. (2012) are replicated. However, as in Experiments 1 and 2, three factors are controlled for: First, a within-subject design is used to determine whether the between-subject design, used by Boyer et al. (2012) influenced their results. Secondly, by using a blocked and a mixed paradigm, the potential effects of response strategies in the blocked experiment is examined. Lastly, to ensure that inconsistencies in the experimental set-up do not shadow the behavioural effects, trials are excluded, which show slight variations in the duration of the stimulus display. If these factors do not influence the biological S-R contingencies, the current studies should replicate the results of Boyer et al. (2012): A BCy effect in the sS-R task and a R-BCy effect in the sOS-R task. However, if these factors influenced the results of Boyer et al. (2012) and biological cues are processed in the same pathway as spatial cues, biological stimuli should elicit a BCy effect in the sS-R and a R-BCy effect in the sOS-R task. Further, Experiment 3 and 4 will examine the temporal pattern of the BCy effects to determine how the automatic and deliberate processes proposed by the dimensional-overlap model and the action-suppression model interact to create the observed effects (Kornblum et al., 1990; R. K. Ridderinkhof, 2002).

3.2 Methods – Experiment 3

3.2.1 Participants

Twenty-five volunteers aged from 19-23 participated in this experiment. Two participants were excluded from the final analysis as equipment error meant the full data-set could not be collected, and one participant was excluded as more than 30 % of trials were erroneous, indicating that they did not fully understand the task. Thus, 22 participants (mean age = 21.3, sd = 1.8, 10 females) were included into the final analysis. On average 6 percent of the trials were excluded from the analysis due to errors in the experimental set-up as well as RTs which were too long or too short. Participants were all undergraduate students from the School of Sports, Exercise and Rehabilitation Sciences at the University of Birmingham and received course credits for their participation. Informed, written consent was received prior to participation and the study was approved by the STEM ethics committee at the University of Birmingham.

3.2.2 Experimental design and analysis – Experiment 3

To assess automatic imitation, Experiment 1 was repeated but the instructions were changed. Participants were instructed to take a third person perspective and to respond to the right/left spatial position of the tapping finger. The sS-R task followed the logic of an S-R paradigm. Participants were instructed to respond according to the left-right spatial position of the imperative stimulus (e.g. if the tapping stimulus finger was to the left-of-centre the participants tapped with their index finger, which was also left-of-centre). BCy was manipulated by using left or right hands as stimuli. If a left hand was shown, all responses were biologically-congruent. If a right hand was shown all responses were biologically-incongruent. The sOS-R task followed the logic of the OS-R paradigm. Participants were instructed to respond with the finger opposite to the left-right spatial position of the imperative stimulus (e.g. if the tapping stimulus finger was to the right-of-centre participants tapped with their middle finger, which was to the right-of-centre as

well). Again, BCy was manipulated by using both left and right hands as stimuli. If a right hand was shown, all responses were biologically-congruent. If a left hand was shown all responses were biologically-incongruent. Else the stimuli, procedure, design, analysis and statistics were identical to Experiment 1.

3.3 Results - Experiment 3

Congruency effects: A RM ANOVA with TASK and biological CONGRUENCY as factors revealed a main effect of TASK, F(1,21)=147.28 p $<$ 0.001, η^2=0.87, indicating that participants reacted faster in the sS-R in comparison with the sOS-R task (MD=63.3 ms, Std error= 5.22, p$<$0.001). A significant interaction between TASK and biological CONGRUENCY was revealed, F(1,21)=92.62, p$<$0.001, η^2=0.81, and follow-up post hoc tests indicated that participants reacted faster during biologically-congruent trials in comparison to biologically-incongruent trials in the sS-R task (MD=17.5, Std error = 1.8, p $<$ 0.001), whereas response times were faster on biologically-incongruent trials in the sOS-R task (MD=17.2, Std error = 2.9, p$<$0.001; Figure 15A).

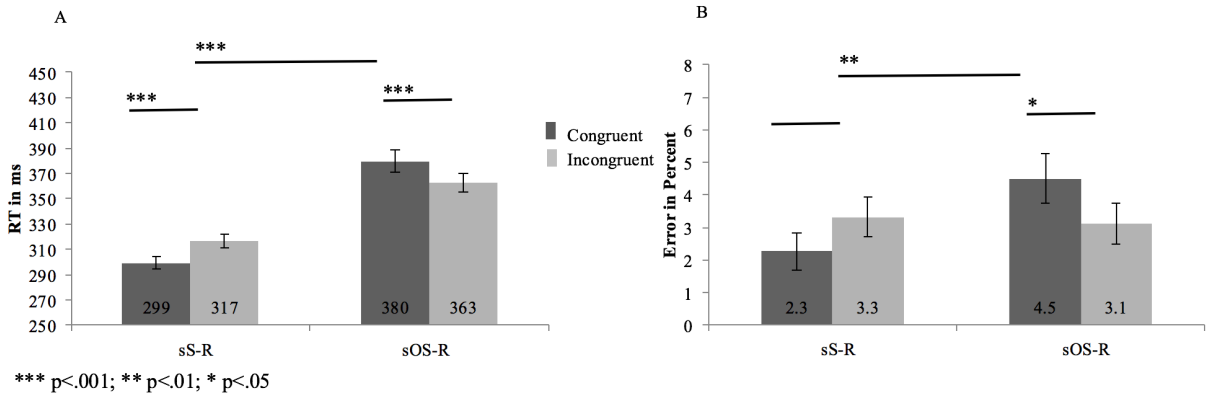


Figure 15: Shows the (A) RTs and (B) error rates in the sS-R and sOS-R tasks of Experiment 3. In the sS-R task RTs were faster in the biologically-congruent condition than in the biologically-incongruent condition. This was reversed in the sOS-R task. In the sS-R task error rates were lowest in the biologically-congruent condition in comparison to the biologically-incongruent condition. This was reversed in the sOS-R task.

Error rate analysis: RM ANOVA showed a significant main effect of task on error

rates, F(1,21)=8.23, p<0.01, η^2=0.28, indicating that participants made less errors in the sS-R compared to the sOS-R task (MD=1 %, Std error=0.4, p < 0.01). The TASK x biological CONGRUENCY interaction was also significant, F(1,21)=10.3, p<0.01, η^2=0.329, and post hoc comparisons showed that participants made more errors in the biologically-incongruent condition compared to the biologically-congruent condition in the sS-R task (MD=1.1 %, Std error = 0.5, p=0.054), which was reversed in the sOS-R task (MD=1.4 % , Std error = 0.5, p<0. 05; Figure 15B)

Reaction time distribution: Consistent with the BCy effect described above, RM ANOVA on the quintile data showed a main effect of TASK on response times, F(1,21)=69.98, p<0.001, η^2=0.77. However, neither the main effect of QUINTILE, F(2,36)=1.33, p>0.05, η^2= 0.06 (GG), or the TASK x QUINTILE interaction, F(1,29)=2.58, p>0.05, η^2=0.11 (GG), were significant. No linear effect was found in the sS-R, F(1,22)=1.862, p>0.05, or sOS-R tasks, F(1,22)=1.848, p>0.05. (Figure 16)

Response accuracy distribution sS-R task: RM ANOVA showed a main effect of biological CONGRUENCY, F(1,21)=5.67, p<0.05, η^2=0.21, no main effect of QUINTILE, F(2,36) =1.69 , p>0.05, η^2=0.07 (GG), and a significant interaction F(4,84)=3.38, p<0.05, η^2=0.14 (Figure 17). Post hoc tests indicated a significant difference in response accuracy between biologically-congruent and biologically-incongruent trials in the first (MD=2.9 %, Std error = 0.9, p<0.01) and third quintile (MD=2.1 % , Std error = 0.8, p<0.05). In both cases, participants made more errors in the biologically-incongruent condition. No linear effect was found for the biologically-congruent, F(1,21)=0.89, p>0.05, or biologically-incongruent conditions, F(1,21)=1.43, p>0.05. Hence, the errors over time did not increase or decrease systematically.

sOS-R task. RM ANOVA showed a main effect of biological CONGRUENCY, F(1,21)=7.87, p<0.05, η^2=0.27, a main effect of QUINITLE, F(2,50) =13.31, p<0.001, η^2=0.39 (GG), and a significant interaction F(4,84)=3.23, p<0.05, η^2=0.13 (Figure 17). Post hoc tests indicated that participants made significant more errors in the biologically-congruent in

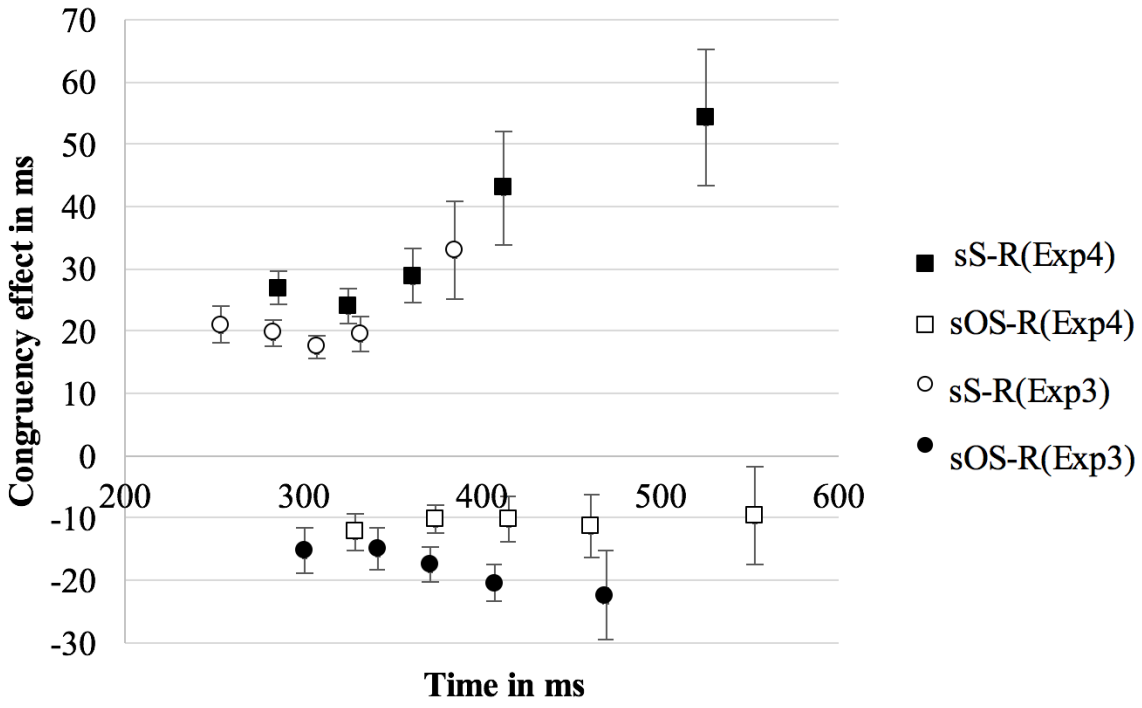


Figure 16: Shows the BCy and R-BCy effects in ms (y-axis) over RT-length (x-axis) from Experiment 3 and 4. In Experiment 3, the BCy effect and its reversal did not reveal any significant results although a trend was visible in the sS-R task. In Experiment 4, the BCy effect in the sS-R task increased with increasing RT. No effect was observed in the sOS-R task.

comparison to the biologically-incongruent condition in the first quintile (MD=4.3 % , Std error = 1.5, $p<0.01$). No other quintiles showed significant effects. Further a linear effect was found in the biologically-congruent, $F(1,21)=23.58$, $p<0.001$ and biologically-incongruent conditions, $F(1,21)=6.38$, $p<0.001$. In both cases less errors were made with increasing RT.

Standard deviation for each condition: RM ANOVA with TASK and biological CONGRUENCY as factors revealed a significant main effect of TASK $F(1,21)=13.43$, $p<0.01$, $\eta^2=0.39$, no main effect of biological CONGRUENCY $F(1,21)=0.001$, $p>0.05$, $\eta^2=0.00$, and an significant interaction, $F(1,21)=5.02$, $p < 0.05$, $\eta^2=0.19$, (Figure 8). Post hoc tests indicated that the standard deviation in the sS-R task was significantly smaller than in the sOS-R task (MD=17.9, Std error =4.9, $p<0.01$). Further, the standard

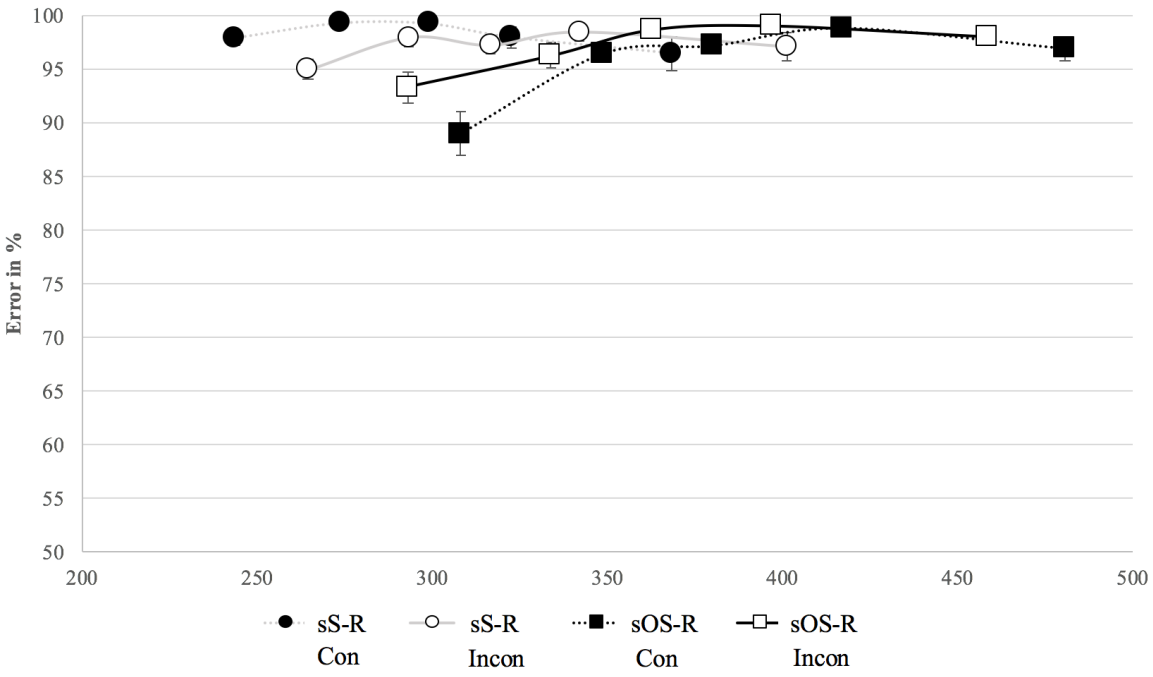


Figure 17: Shows the response accuracy in percentage (y-axis) over RT-length in ms (x-axis) from Experiment 3. In the sS-R task more fast errors were made in the biologically-incongruent condition in comparison to the biologically-congruent condition. This was reversed in the sOS-R task.

deviation in the sS-R task was larger in the biologically-incongruent in comparison to the biologically-congruent condition. However, this effect did not reach significance (MD=5.8 ms, Std error=3.8, $p>0.06$). No difference between the standard deviation of biologically-congruent and biologically-incongruent trials were found in the sOS-R task (MD=5.9, Std error = 3.8, $p>0.05$; Figure 8).

3.4 Discussion - Experiment 3

3.4.1 BCy and R-BCy effects

Experiment 3 used a within-subject blocked design to measure automatic imitation effects in sS-R and sOS-R tasks. In general, the RTs in sS-R task were more than 120 ms faster than the RTs in the study of Boyer at al. (2012). This only decreased slightly for the sOS-R task, where the difference between studies were approximately 80 ms. In the sS-R task the current experiment revealed a BCy effect. That is, participants reacted faster when

the biological stimulus was congruent in comparison to incongruent with the response. This effect has been shown repeatedly and is called automatic imitation (Heyes, 2011). The automatic imitation effect in the present Experiment was slightly smaller (18 ms in Experiment 1 vs 29 ms in the Experiment of Boyer and colleagues) than in the study of Boyer et al.(2012). Automatic imitation effects are ranging from almost 100 ms (Brass et al., 2000) over 40 ms (Gowen et al., 2010) to 29 ms (Press et al., 2005). Hence, the current automatic imitation effect is rather small but still very consistent.

More importantly, the sOS-R task showed a R-BCy effect. This means that biological stimuli are affected by logical recoding and deliberate short-term S-R associations (Hedge & Marsh, 1975; R. K. Ridderinkhof, 2002). According to the computation model of Sauser and Billard (2006), this indicates that spatial and biological stimuli use a single-route to elicit the observed effects. These findings contradict the results of Boyer et al. (2012), who did not find any BCy or R-BCy effects for task-irrelevant biological cues in the sOS-R task. Hence, using a within-subject design changed the results.

The R-BCy effect was 17 ms, which almost equals the screen refresh rate (16 ms). In Chapter 2, it was explained how fluctuations in the refresh rate of a monitor could influence how long a stimulus is on the screen. Although these variations only prolong the duration of a stimulus-display by milliseconds, they can easily affect effects as small as the R-BCy effect. The current experimental set-up could detect these variations of the screen refresh rate so that the affected trials could be excluded from the analysis. Boyer et al. (2012) did not mention that any precautions like these were taken in their study. Therefore, it is likely that this also affected the differences in the results, especially since the R-BCy effect was as small as one screen refresh rate. This is the first behavioural study, which based on hypotheses from computational models provide clear evidence that spatial and biological stimuli are processed alike.

3.4.2 The processes underlying SCy and R-SCy effects - RTs over Time

The temporal pattern of the BCy and R-BCy effects were analyzed to gain a better understanding about the underlying processes. The delta plots of the BCy and R-BCy effects did not show any significant results. Hence, there was no increasing or decreasing BCy and R-BCy effects with increasing RTs. However, visual inspection of the plots showed a trend that the BCy effect may increase with increasing RT in the sS-R task. Since the RTs in the current study were shorter than in the study of Boyer et al. (2012), it could explain why they found a rising delta plot for biological stimuli in the sS-R task, which was not replicated in Experiment 3. In mixed designs, RTs increase, and therefore it is hypothesized that the effect could become significant in Experiment 4. Importantly, the R-BCy effect was present from the fastest RTs onwards, which would suggest that short-term S-R associations influenced the automatic congruent processes before participants could respond (R. K. Ridderinkhof, 2002).

3.4.3 The processes underlying SCy and R-SCy effects - Response accuracy over Time

As in Experiment 1 and 2, the pattern of the fastest errors resembled the pattern of the BCy and R-BCy effects. That is, in the sS-R task participants made more fast errors in the biologically-incongruent condition in comparison to biologically-congruent condition. This tendency switched in the sOS-R task. This means that fast responses in the sOS-R task were not in accordance with the learned S-R associations, but in favour of the response rule determined by the task instructions. Hence, the processing of task-irrelevant biological stimuli was affected by logical recoding before responding occurred.

In conclusion, the experiment, which used a within-subject design provided evidence that biological cues are affected by logical recoding, which shows that biological cues are not automatically mapped onto the observer's motor system. In contrast, biological stimuli are likely processed in a similar network as spatial stimuli (Sauser & Billard, 2006).

3.4.4 Aims of Experiment 4

The following experiment will assess the reliability of the BCy and R-BCy effects by using a mixed paradigm. Since blocked designs allow for the formation of response strategies (Catmur and Heyes, 2011), this is a necessary step to confirm that the results from Experiment 3 are reliable. Further, using a mixed design could evoke potential differences between BCy and SCy effects. Whereas spatial cues usually trigger similar effects in blocked and mixed designs, no study has yet assessed the influence of experimental design on the BCy effect. Hence, it is still questionable whether biological cues will be affected by the increased task difficulty in the upcoming experiment.

3.5 Methods - Experiment 4

3.5.1 Participants

Twenty-six right-handed volunteers participated in Experiment 4. Five participants were excluded from the analysis (three due to equipment error, one that showed clear signs of sleepiness during the experiment and one who made more than the allowed numbers of errors). Thus, 21 participants (mean age = 22-37, sd = 3.2, 9 females) were included into the analysis. On average 10 percent of the trials were excluded from the analysis.

3.5.2 Experimental design and analysis

Experiment 3 was repeated but with the mixed design of Experiment 2. A red or a green frame (visual angle 2.5°), was presented around the edge of the screen throughout the duration of each trial. The colour indicated whether participants needed to perform the sS-R task or sOS-R task. The colour – task relationship was counter balanced across subjects. Else the stimuli, procedure, design, analysis and statistics were identical to Experiment 3. Trials were excluded, if the observed movement was presented more than 1 ms outside the normal 133 ms.

3.6 Results - Experiment 4

Congruency effects: RM ANOVA revealed a main effect of TASK on the response times, F(1,20)=67.85, p<0.001, η^2=0.77, indicating that participants responded faster in the sS-R task in comparison with the sOS-R task (MD=53.3, Std error=6.5, p<0.001; Figure 18A). A significant effect of biological CONGRUENCY, F(1,20)=13.92, p<0.001, η^2=0.41, showed that response times were slower for biologically-incongruent trials in comparison to biologically-congruent trials (MD=9.5 ms, Std error=2.6, p<0.01). A significant interaction between TASK and biological CONGRUENCY F(1,20)=40.70, p<0.001, η^2=.67, and post hoc comparisons revealed that response times were faster during biologically-congruent trials in comparison to biologically-incongruent trials in the sS-R task (MD=29.03 ms, Std error = 4.349, p<0.001), whereas in the sOS-R task participants were faster during biologically-incongruent trials (MD=9.9 ms, Std error = 3.6, p<0.05; Figure 18A)

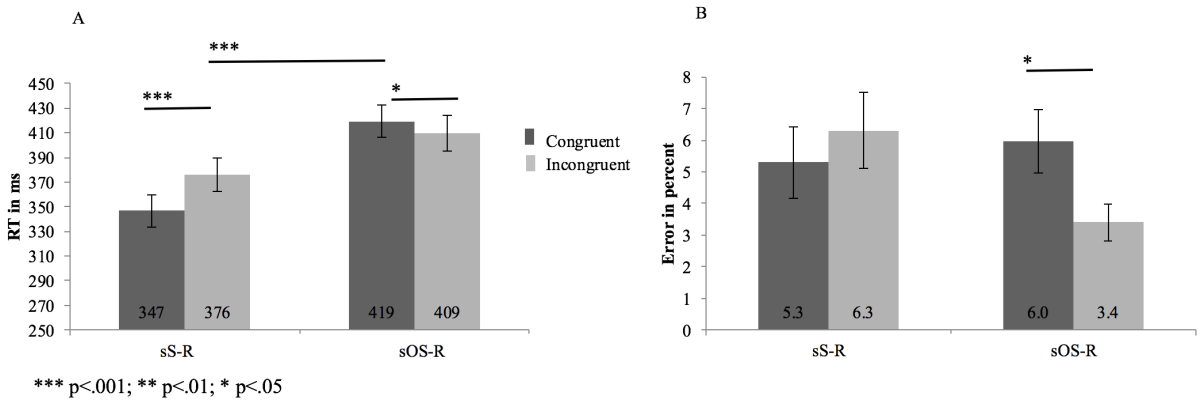


Figure 18: Shows the (A) RTs and (B) error rates in the sS-R and sOS-R tasks of Experiment 4. In the bS-R task RTs were faster in the biologically-congruent condition than in the biologically-incongruent condition. This was reversed in the sOS-R task. In the sS-R task error rates were lowest in the biologically-congruent condition in comparison to the biologically-incongruent condition. This was reversed in the sOS-R task.

Error rates analysis: RM ANOVA with TASK and biological CONGRUENCY as factors only showed a significant interaction, F(1,20)=6.54, p<0.05, η^2=.246 (Figure 18B). Post hoc tests showed that participants made significantly more errors in the biologically-

congruent condition compared to the biologically-incongruent condition in the sOS-R task (MD=2.6 %, Std error = 1.0, p<0.05). No difference was found in the sS-R task (MD=1.0 %, Std error = 0.8, p>0. 05; Figure 18B).

Reaction time distribution: RM ANOVA showed a significant main effect of TASK, F(1,20)=57.00, p<0.001, η^2=0.74. This confirmed that the BCy effect, across all quintiles, was positive in the sS-R task and negative in the sOS-R task (Figure 16). Importantly, however, a significant interaction, F(2,44)=3.79, p<0.05, η^2=.16 (GG), was also observed, showing that the BCy effect followed a different pattern in the sS-R and sOS-R tasks. A significant linear effect was found in the sS-R task (F(1,20) = 6.727, p < 0.05), but not in the sOS-R task (F(1,20) = 0.7, p > 0.05) indicating whilst the BCy effect in the sS-R task increased as the RTs increased, the R-BCy effect in the sOS-R task remained stable over all quintiles (Figure 16).

Response accuracy distribution sS-R task: RM ANOVA showed a main effect of QUINTILE, F(2,35) = 13.09 p<0.001, η^2=0.39 (GG), indicating that the amount of errors increased with longer RTs across the biologically-congruent and biologically-incongruent conditions (Figure 19). No significant interaction was found between QUINTILE and biological CONGRUENCY F(3,55)= 0.33 p>0.05, η^2=0.02 (GG). Additionally, linear effects were found in the biologically-congruent, F(1,20)=26.23 p<0.001, and biologically-incongruent conditions, F(1,20)=11.07 p<0.01. In both cases the amount of errors increased with increasing RT.

sOS-R task. RM ANOVA showed a main effect of QUINTILE, F(2,33) =6.37 p<0.001, η^2=0.24 (GG), indicating that the amount of errors decreased with increasing RT. No interaction between biolgical CONGRUENCY and QUINTILE was revealed, F(4,80)=1.74 p>0.05, η^2=0.08. Additionally a linear effect was found in the biologically-incongruent condition F(1,20)=10.18 p>0.01 showing that the error rate decreased with increasing RT. No linear effect was found in the biologically-congruent condition F(1,20)=0.045 p>0.05 (Figure 19).

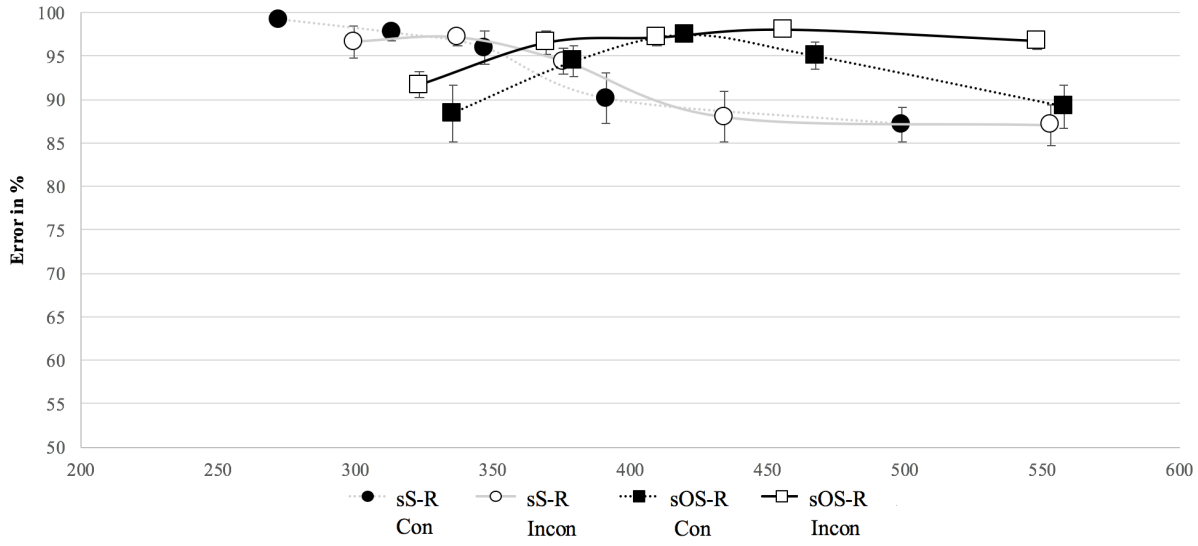


Figure 19: Shows the response accuracy in percentage (y-axis) over RT-length in ms (x-axis) from Experiment 4. In the sS-R task more fast errors were made in the biologically-incongruent in comparison to the biologically-congruent condition. This was reversed in the sOS-R task. None of these effects became significant.

Standard deviation for each condition: RM ANOVA with TASK and biological CONGRUENCY as factors revealed no significant main effect of TASK,$F(1,20)=1.98$, $p > 0.05$, $\eta^2=0.09$, or biological CONGRUENCY ,$F(1,20)=2.77$, $p > 0.05$, $\eta^2=0.12$, and no interaction, $F(1,20)=1.85$, $p > 0.05$, $\eta^2=0.85$. Post hoc tests confirmed that there was no difference between standard deviations for biologically-congruent and biologically-incongruent conditions in the sS-R (MD=8.0, Std error = 4.6, $p>0.05$) and sOS-R (MD=0.5, Std error = 2.9, $p>0.05$) tasks (Figure 8).

3.7 Discussion – Experiment 4

The present experiments were set-up to measure BCy and R-BCy effects. Experiment 4 used a mixed within-subject design to assess whether response strategy formation influenced the results observed in Experiment 3.

3.7.1 BCy and R-BCy effects

In comparison to Experiment 3, RTs increased by approximately 50 ms. However, a BCy effect in the sS-R task was still detected, and in comparison to Experiment 3, where the BCy effect was 18 ms, it had increased to 29 ms in Experiment 4. Hence, the size of the effect was comparable to BCy effects mentioned in other studies (Press et al., 2005; Boyer et al., 2012).

More importantly, Experiment 4 and 3 revealed a R-BCy effect in the sOS-R task. In comparison to Experiment 3, where the R-BCy effect was -17 ms, it had decreased to -10 ms in Experiment 4. Despite such slight variations, it is important that Experiment 3 and 4 showed similar results since it shows that the BCy and R-BCy effects are very stable phenomena, which are not influenced by additional mental processes related to task switching (Proctor & Fisicaro, 1977; Los, 1996). This is important since stable congruency effects across blocked and mixed tasks have been revealed for non-biological cues (Proctor & Vu, 2002; Proctor et al., 2011) such as in Experiment 1 and 2 as well.

Sauser and Billard (2006) proposed that only a single-route model can account for the R-BCy effect in the sOS-R task. In this model, biological and spatial task-irrelevant stimuli are processed in the same route. In the PPC a response is mapped to the perceived stimulus. However, this process is controlled by the input from the PFC. The input from the PFC integrates the S-R rules from the task instructions into the S-R mapping. This facilitates responding in the condition, which is in accordance with the task instructions. Therefore, responding in the incongruent condition in comparison to the congruent condition improves, when the task asks participants to respond in a non-matching manner. This is the first study, which finds no dissociation between the processing of biological and spatial stimuli by using an OS-R task. Although, Boyer et al. (2012) used the identical paradigm, they did not find the R-BCy effect in the sOS-R task.

Since Experiment 3 and 4 both elicited R-BCy effects, it can be concluded that response strategies did not influence task performance (Catmur and Heyes, 2011). Therefore, the use of a within-subject design or the precise experimental set-up increased the internal

validity and the reliability of the current experiments and, thus, revealed the R-BCy effect in the sOS-R task (Charness et al., 2013).

3.7.2 The processes underlying BCy and R-BCy effects - RTs over time

The automatic imitation effect in the S-R tasks increased with slower RTs. However, this effect only reached significance in Experiment 4, but a tendency was also observed in Experiment 3 [17]. This pattern replicated the findings of Boyer et al. (2012). As in Experiment 1, the rising delta plot in the S-R task can be interpreted differently depending on the applied theory. As explained in the Discussion of Experiment 1 and 2, Wiegand et al. (2005, 2007) proposed that congruency effects can be separated into two distinct types depending on the experimental design. For cognitive congruency effects, there is no inherent connection between the hemisphere primarily activated by the task-irrelevant stimulus and the hemisphere primarily activated by the response. Therefore, the S-R mapping evolves slower in comparison to the S-R mapping guiding the visuomotor congruency effect. This results in a more pronounced cognitive congruency effect with increasing time. Since the present paradigm used unimanual responses there was no inherent connection between hemispheric activity during stimulus perception and response execution. Hence, the resulting cognitive BCy effect increased with time. According, to the action-suppression model, which has been described in the Introduction to Experiment 1 and 2, a rising delta plot could also indicate that deliberate short-term S-R associations are contributing to the observed effect (De Jong et al., 1994; Bertenthal et al., 2006; R. K. Ridderinkhof, 2002). Lastly, an increasing delta plot could be attributed to the complexity of the stimulus, which requires more processing time and therefore its effects on behaviour increase with time (Brass et al., 2001; Catmur & Heyes, 2011). Which of these accounts are correct, still needs to be determined, but this would extend the scope of the current thesis.

Interestingly, the R-BCy effect remained stable with increasing RT, which could indi-

[17] Since no significant difference was found between the variance of the RTs in biologically-congruent and biologically-incongruent conditions, the effects were not explained by such differences in the data.

cate that the R-BCy effect had reached a sealing effect. This could either suggest that deliberate S-R mappings do not affect the R-BCy strongly or that counter-mechanisms are working against the R-BCy effect, which prevents it from increasing. Further, studies would need to examine these hypotheses.

3.7.3 The processes underlying BCy and R-BCy effects - Response accuracy over time

Lastly, Experiment 3 showed that the response accuracy for the fastest RTs was in line with the observed BCy and R-BCy effects: in the sS-R task participants made more fast errors in the biologically-incongruent condition. In contrast, participants made more fast errors in the biologically-congruent in comparison to the biologically-incongruent condition in the sOS-R task. In Experiment 4, there was no significant difference between the number of fast errors in the biologically-congruent and biologically-incongruent conditions in the sS-R and sOS-R tasks. However, from visual inspection of Figure 19 similar trends as observed in Experiment 3 (Figure 17) are noticeable. These results show that long-term S-R associations guided fast responses in the sS-R task but that these were controlled in the sOS-R task. Accordingly, deliberate short-term S-R processes, which are formed by the task instructions, influenced responding in the sOS-R task before participants started responding. These results confirm that biological stimuli are not processed in a direct-matching pathway, which always provokes imitation. Instead, biological stimuli, as their spatial counterparts, are processed in a pathway, which is influenced by external factors such as task instructions. These results confirm previous findings that the perception of biological actions trigger different activation in the mirror neuron system, depending on the context in which these actions are being performed. (Wunn and Schubotz, 2012).

As in Experiment 1 and 2, the findings that automatic processes can be suppressed does not mean that they are not important for behaviour, at all. In general, people react faster and more accurate in S-R than OS-R tasks regardless of whether the task-relevant stimulus is biological or spatial (Hasbroucq & Guiard, 1991; Hedge & Marsh, 1975; Proctor & Pick,

2003). This was also observed in Experiment 1 and 2 where conscious imitation was faster and more correct than conscious counter-imitation. In Experiment 3 and 4, participants performed better in the sS-R task in comparison to the sOS-R task as well. Again, the differences in performance between tasks (sS-R vs sOS-R) explained more of the variance in the data than the differences in BCy. This means that people have a strong tendency to react in accordance with the observed stimulus and when this tendency needs to be inhibited, as in the OS-R task, performance degradation can be expected. Many other studies have reported a similar increase in RTs and error rates under similar circumstances and have suggested that these are caused by top-down control mechanisms during the OS-R task (Proctor & Pick, 2003).

In sum, the experiments showed that biological cues are not processed in a direct-matching pathway, which instantaneously matches the observed movement onto the observer's own motor system. In contrast, it is likely that more deliberate, short-term S-R associations influence responding to biological stimuli in accordance with the single-route model (Sauser and Billard, 2006).

3.8 General Discussion – Experiment 1 to 4

In the General Introduction, it was described that generic S-R contingencies could generate automatic imitation. For example, it has been suggested that BCy and SCy effects are elicited due to common codes between perceived stimuli and executed actions. This idea is not new but stems from pioneering theories explaining unconscious S-R mappings. Theories like the dimensional overlap model (Kornblum et al., 1990) or the ideomotor theory (James, 1890) described that actions are triggered by the 'imagination' of action effects. A perceived movement (biological or non-biological) is automatically converted into its movement effects, which automatically generates an action. Despite the similar theoretical explanation of SCy and BCy effects, there is a strong opposing view suggesting that biological S-R contingencies have evolved separately to promote social interaction (Rizzolatti & Craighero, 2004). The discovery of mirror neurons further strengthened this

hypothesis since these neurons provided the mechanisms by which automatic imitation could occur. Behavioural studies have produced very inconclusive results: whereas some studies show that RTs to biological cues are faster than to spatial cues (Jonas et al., 2007; Press et al., 2005), that BCy effects are larger than the SCy effects (Brass et al., 2001, 2005), others have found no differences when reacting to spatial and biological stimuli (Jansson et al., 2007) or faster RTs to spatial in comparison to biological stimuli (Van Elk, Van Schie, & Bekkering, 2011; Newman-Norlund, 2010).

Due to these rather conflicting results, Sauser and Billard (2006) suggested using OS-R tasks to distinguish how spatial and biological stimuli are processed and formulated two distinct computational models. The single-route model predicted that biological and spatial stimuli are processed alike. The central aspect of the model was that the S-R mappings of the task-irrelevant stimuli were influenced by top-down cognitive mechanisms. These controlled the long-term S-R mappings by incorporating the response rule defined by task instructions. In contrast, to the single-route model, the direct-matching model incorporated an additional pathway for biological stimuli and therefore the observed biological stimuli always elicited imitation. Both models simulated a congruency effect for biological and spatial stimuli in the S-R task. However, their predictions differed for the OS-R task. Whereas the single-route model simulated a reversed congruency effect for biological and spatial stimuli, the direct-matching model predicted a reversed congruency effect for spatial and no effect for biological cues.

3.8.1 Biological and spatial S-R mappings during congruency and reversed congruency effects

The present study was set-up to test the predictions of these models to understand whether biological and spatial cues are processed differently or alike. Thereby, the paradigm of Boyer et al. (2012) was applied, since it did not include common limitations often seen in the automatic imitation literature (See, Introduction - Experiment 3 and 4). In contrast to the study of Boyer et al. (2012), the current experiments used a within-subject design

with blocked or mixed trials with an experimental set-up that detected slight variations in the stimulus display.

Across four experiments we found a SCy effect in the bS-R tasks and a R-SCy effect in the bOS-R tasks (Experiments 1 and 2). Additionally, BCy effects were found in the sS-R tasks and R-BCy effects were found in the sOS-R tasks (Experiments 3 and 4). SCy and R-SCy effects have been replicated repeatedly using S-R and OS-R paradigms (De Jong et al., 1994; Hasbroucq & Guiard, 1991; Lu & Proctor, 1995; H. H. Zhang, Zhang, & Kornblum, 1999). Similarly, finding a BCy effect in the sS-R task is very common (Brass et al., 2000, 2001; Catmur & Heyes, 2011). However, the present study is the first to show that task-irrelevant biological stimuli also elicit R-BCy effects. Both the blocked (Experiment 3) and the mixed experiments (Experiment 4) revealed the effect, which means that R-BCy effects are not influenced by working memory (Proctor & Fisicaro, 1977; Los, 1996). Whereas the R-BCy effect decreased in the mixed (Experiment 4) in comparison to the blocked (Experiment 3) experiment, the R-SCy effect increased in the mixed (Experiment 2) in comparison to the blocked experiment (Experiment 1). Since the mixed design draws on cognitive control mechanisms due to task switching (Proctor & Fisicaro, 1977; Los, 1996), these results could indicate that control mechanisms influence the spatial and biological effects differently.

The presence of the reversal effects for biological and spatial stimuli has wide ranging consequences on the interpretation of biological cueing effects. Accordingly, biological stimuli do not always cause an imitative response through a direct-matching route as suggested by proponents of the mirror neuron theory (Iacoboni, 2005). In contrast, the BCy effects depend on the task instructions. If the participants are prompted to respond in an incompatible manner, the biologically-incongruent stimulus appears to be facilitating the response through its fit with the temporarily established response rule. A phenomenon which has been discovered for spatial stimuli many years ago (Hedge & Marsh, 1975).

Our results contrast the nativist view, which says that humans have developed a specialized mirroring circuit to process biological stimuli, which has evolved through natural

selection to understand peoples' actions (Rizzolatti & Craighero, 2004; Boyer et al., 2012; Scheutz & Bertenthal, 2012). This nativist view has been supported by findings that infants as young as a couple of hours engage in imitation (Meltzoff & Moore, 1989). For more than 20 years conflicting studies have created confusing evidence whether neo-natal infants indeed imitate. Very young infants seemed to imitate adults performing tongue protrusions. But increased tongue protrusions were also revealed when non-biological stimuli were presented (Jacobson, 1979). Therefore, tongue protrusion is likely an indicator for excitement rather than an example of imitation (Jones, 2006). A recent longitudinal study testing 100 infants between one and nine weeks found no evidence that people are born with an innate ability to imitate (Oostenbroek et al., 2016). Therefore, the nativist view has been replaced with more empirical accounts summarized in the next paragraph.

3.8.2 Associative learning and S-R mappings

Since it is unlikely that humans are born with a mechanism to process biological stimuli a more empirical theory related to the ideomotor theory has gained approval: The Associative learning (ASL) account suggests that humans learn links between perceived visual stimuli (biological and non-biological) and executed movements and when a sensory-action link has been encoded perception of a stimulus triggers the associated movement (Press, Cook, Blakemore, & Kilner, 2011). Evidence in favour of the ASL theory comes from training studies. In simple-response paradigms (See, General Introduction) participants are trained to perform incompatible actions instead of compatible actions to imperative biological stimuli. Brain areas that are originally activated when participants perform the compatible response, are activated by the incompatible response after training (Catmur et al., 2007). As described throughout the thesis, the perception of actions trigger increased activation (larger MEPs) of the corresponding muscle in the observer. However, when pairing arbitrary non-biological stimuli such as tones, colours or shapes with a motor output and training participants repeatedly with this association, the M1 increases activity

when presenting the tone, colour or shape by itself (Petroni, Baguear, & Della-Maggiore, 2010). These effects are stressed by an fMRI study showing that mirror neuron areas (vPMC, IPL) are activated by shapes, if these shapes have been associated with movements (Press, Catmur, et al., 2012). These results show that the human motor system is not only automatically activated by observed biological movements but also by non-biological stimuli, if these are associated with a movement through previous experience. Therefore, it is likely that imitation of biological stimuli is learned through experience as well. By observing their own hand movements people are often exposed to the observation of actions while they perform the same action. Hence, imitation is likely just an extensively practiced behaviour similar to other (non-biological) S-R mappings.

3.8.3 The function of automatic imitation

However, only because spatial and biological S-R mappings are likely relying on similar cognitive mechanisms, imitation could still be a necessary and meaningful behavior. Here, three different views exist. First, the nihilist account suggests that imitation does not have any function over and above other non-biological S-R contingencies. However, this is quite unlikely when looking at the large amount of research showing that S-R mappings are likely tuned towards biological stimuli (Press et al., 2011) and likely promote social well-being or/and action understanding.

The "social glue" account suggests that imitation strengthens relationships (Chartrand & Bargh, 1999; Chartrand & Lakin, 2013). Findings showing that imitation increase bonding, kindness and agreeableness between individuals support this theory (Van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009; Guéguen, Martin, & Meineri, 2011). Even infants are more helpful by handing an experimenter a pen, when being imitated by the experimenter (Carpenter, Uebel, & Tomasello, 2013). Hence, imitation could have a crucial function over and above non-biological S-R mappings.

Further, the simulation account claims that imitation helps understanding behaviour to interact with people correctly. Evidence comes from studies showing that imitation

of facial expressions is directly related to the understanding of the other person's state (Wood, Rychlowska, Korb, & Niedenthal, 2016). On the other hand, if a person cannot form natural facial expressions because of Botox injections, a bystander experiences difficulties understanding this person's emotions (Neal & Chartrand, 2011). Although the simulation theory works well for facial expressions, it fails to explain how people understand perceived actions by the mere input of movement trajectories. Not all actions only convey a single meaning. For example, seeing a person waving with the hand could mean that he/she is trying to get a taxi or that he/she is greeting a friend (Press et al., 2011). Therefore, additional information besides the pure movement output is required to understand the correct meaning of the observed behaviour. To limit the range of possible observed actions, it is crucial to form previous expectations based on the context, and these predictions enable correct action understanding through action simulation (Press et al., 2011).

Regardless which theory is correct, these reviewed studies, as well as the present results, reveal an important shift in the assessment of the mirror neuron system. Instead of asking whether mirroring is a unique behaviour elicited by biological stimuli, one should concentrate on examining the function of mirroring.

3.8.4 The processes underlying SCy/BCy and R-SCy/R-BCy effects - RTs over Time

In the current study, we used distributional analyses (Ratcliff, 1979) to get a better understanding of the interaction between automatic and deliberate processes during S-R mapping. It was especially of interest whether automatic congruent responses were controlled by short-term S-R associations whenever participants performed an OS-R task.

As noted in the Introduction of Chapter 2, the presence of reversal effects in OS-R tasks does not exclude the possibility that automatic processes might be involved. The dimensional overlap and the action-suppression models propose that an automatic (long-term S-R associations) and a deliberate route (short-term S-R associations) interact to elicit

the congruency and reversed congruency effects. Whereas the automatic route produces fast congruent responses, the deliberate route is slower and takes task instructions into account (R. K. Ridderinkhof, 2002). By assessing the temporal dynamics of the congruency and reversed congruency effects, it is possible to estimate how much the automatic and deliberate processes were involved in the S-R mappings. The action-suppression model proposes that automatic stimulus-congruent responses should be present when reacting fast. Hence, one should observe an inclination to respond congruently in S-R or OS-R tasks for fast RTs.

In all experiments the congruency effects and reversed congruency effects increased or remained stable with time. As pointed out in the Discussions of Experiment 1 and 2 and Experiment 3 and 4, rising delta plots in the S-R tasks, could be caused the unimanual paradigm, which triggers cognitive congruency effects (Wiegand & Wascher, 2005). Secondly, the deliberate and short-term S-R mappings could have supported the bias toward the congruent response (R. K. Ridderinkhof, 2002). Lastly, it has been argued that biological stimuli are very complex and that participants require much time to process them. Therefore, the effect of the task-irrelevant biological stimuli increase with time (Catmur & Heyes, 2011).

The delta plots in the OS-R tasks provided a better insight into the deliberate vs. automatic processes. In most cases, the reversed congruency effect increased with increasing RTs, although a quadratic relationship was also observed (Experiment 2). This is in accordance with the finding of Dejong (1994). An increase in the reversed congruency effect with increasing RT is a sign that deliberate S-R mappings guide responding. The R-BCy and R-SCy effects were present from the fastest RTs onwards, which was also in accordance with Dejong (De Jong et al., 1994). This shows the logical recoding was accomplished before the participant reacted.

3.8.5 The processes underlying SCy/BCy and R-SCy/R-BCy effects - Response accuracy over time

Evidence that logical recoding influenced long-term S-R associations in the OS-R tasks before a response was executed also came from the temporal pattern of the error rates. Here, fast errors should occur in the incongruent condition regardless of the task (S-R/OS-R), if people have a fast tendency to respond with the learned S-R mapping. In the S-R tasks, the incongruent conditions indeed showed more fast errors than the congruent conditions. However, in the OS-R tasks, this pattern was reversed, so that participants made more fast errors in the congruent in comparison to incongruent conditions, setting aside the nature of the task-irrelevant stimulus. Although these results indicate the long-term S-R mappings contributed to the SCy and BCy effects, they also show that short-term S-R response associations influenced responding in the OS-R tasks before participants could react. Importantly, spatial and biological task-irrelevant stimuli revealed very similar patterns in both distributional analyses, which means that biological and spatial stimuli were equally influenced by deliberate processes. This finding stresses, that spatial and biological stimuli are processed alike using learned S-R contingencies, which are controlled by higher-order processes.

3.8.6 Differences between S-R and OS-R tasks

In all studies, the performance was better in the S-R tasks than in the OS-R tasks. This means that participants reacted faster and made fewer errors while making a compatible response in comparison to an incompatible response. Of course, these responses were not unconscious as the effects triggered by the task-irrelevant stimuli. However, they still show that participants performed better when using long-term S-R mappings.

Interestingly, the difference between RTs in the bS-R and bOS-R tasks was larger than the difference in RTs between sS-R and sOS-R tasks, indicating that it was more difficult to perform a counter-imitative movement than a counter-spatial movement. As mentioned in the General Introduction, Heyes (2011) argued that conscious and unconscious imitation

draws on similar cognitive mechanisms. Therefore, differences between bS-R and bOS-R tasks could provide valuable insights into the automatic processes contributing to the BCy and R-BCy effects in the sS-R and sOS-R tasks.

3.9 Conclusion - Experiment 1 to 4

Experiment 1 to 4 assessed SCy, R-SCy, BCy and R-BCy effects to understand whether biological and spatial task-irrelevant stimuli are processed alike. The computational models of Sauser and Billard (2006) clearly showed that an OS-R task is necessary to distinguish between spatial and biological S-R mappings, since spatial and biological stimuli always elicit similar effects in the respective S-R tasks. However, the present experiments revealed R-SCy and R-BCy effects in the OS-R tasks as well. This shows that task-irrelevant spatial and biological stimuli are influenced by logical recording in accordance with the single-route model (Hedge & Marsh, 1975; Sauser & Billard, 2006). With these results the present study speaks against the nativist view and in favour of theories explaining that spatial and biological stimuli are processed alike. Lastly, whereas, there were clear indications that spatial and biological stimuli were processed in accordance with long-term S-R associations in the S-R task, these were controlled in the OS-R task, indicating that logical recoding occurred before responses were executed.

3.10 Preview: studying automatic imitation using MEG

Although the present study showed convincing evidence that biological and spatial stimuli are processed alike, imaging studies are required to validate the results. Behavioural studies only measure neural processes indirectly by examining differences or similarities in responses across conditions.

As mentioned in the General Introduction, neuroscientific research has produced convincing results that humans have developed unique neural mechanisms to process biological stimuli (Di Pellegrino et al., 1992), including fMRI and TMS studies assessing the neural correlates of spatial and biological S-R mapping (Bien et al., 2009; Brass et al.,

2005; Catmur et al., 2009; Heyes, 2011; Cook et al., 2014; Simpson et al., 2014). Since the behavioural results from Experiment 1 to 4 clearly indicated that spatial and biological stimuli are processed alike they contradict most of these imaging studies. However, as mentioned above there is evidence of TMS studies showing that it is possible to elicit mirror results from counter-imitative movements, which indicate that the mirror neuron system is somewhat flexible (Catmur et al., 2007). In any case, it is critical to understand whether different neural mechanisms could elicit similar behavioural effects for spatial and biological stimuli.

To date, no study has used MEG recordings while measuring BCy and SCy effects using an S-R paradigm, despite its excellent temporal and good spatial resolution. In the General Introduction, we argued that these characteristics make MEG the best tool to pick up the fast-paced processes guiding automatic imitation while locating a spatially complex neural network. In Chapter 4, Experiment 2 is replicated while using MEG. First findings from imaging studies assessing spatial S-R contingencies are introduced, before the experiment and the results are explained and discussed. In Chapter 5, Experiment 4 will be repeated while recording MEG. The Chapter will follow the same structure as Chapter 4, but with a general discussion at the end, which compares the results from Experiment 5 and 6. We decided to use the mixed design for the MEG studies since it prolonged RTs considerably in experiments 2 and 4 in comparison to experiments 1 and 3. Since it is of interest to assess the neural correlates leading up to automatic imitation, prolonging the RTs allows us to include a larger data segment, which increases the frequency resolution and hence the accuracy of the data.

4 Chapter 4

4.1 Introduction - Experiment 5

4.1.1 The neural correlates of SCy

The following study is set-up to assess the neural correlates underlying the SCy and R-SCy effects. These neural processes will later be compared to the neural mechanisms associated with the BCy and R-BCy effects, to answer the question whether biological and spatial cues are processed by similar neural networks. In Experiment 1 and 2, SCy effects were revealed in the bS-R tasks. These findings suggest that the task-irrelevant spatial cues automatically triggered the congruent responses as a consequence of associative learning or dimensional overlap (Press et al., 2011; Kornblum et al., 1990). During spatially-incongruent trials these automatic responses needed to be inhibited, and therefore much of the research described below focuses on the neural processes related to inhibition or cognitive control.

Also, R-SCy effects were found in the bOS-R tasks, which suggests that recoding of the S-R associations occurred since the task instructions prompted participants to respond in an incompatible manner (Sauser & Billard, 2006; Hedge & Marsh, 1975). In such cases, the spatially-incongruent task-irrelevant stimuli were beneficial for responding, whereas the spatially-congruent stimuli needed to be inhibited. Unfortunately, very few studies have assessed the neural signature during the R-SCy effect (Cao, Cao, Yue, & Wang, 2017). Therefore, findings from Simon-like S-R tasks will help to form hypotheses about the neural signature exhibited during the bS-R and bOS-R tasks. Studies using ERPs or time-frequency analyses will be reviewed. The focus is on the latter since alpha and beta oscillations have been associated with MN activity, whereas theta activity could have a unique role in spatial cue processing (Hari et al., 1998; Kessler et al., 2006; Cohen et al., 2008). ERP studies are therefore summarized in Appendix D Section: ***Event-Related Potentials and SCy***. There, the focus is on the lateralized readiness potential (LRP), the N2 and the P300 components. This chapter will continue summarizing the findings

from studies, which have applied time-frequency analyses.

4.1.2 Spatial S-R mapping and theta band changes

Theta activity is most likely generated in the midcingulate cortex and (pre)-SMA and is considered a neural indicator for higher-order cognitive processes during memory retrieval, memory encoding, working memory processes or top-down control mechanisms (Nigbur, Ivanova, & Stürmer, 2011; Cohen et al., 2008). Frontal theta power has repeatedly been shown to increase more in the spatially-incongruent condition in comparison to the spatially-congruent condition in a Simon-like S-R task between 200 to 400 ms after stimulus presentation (Nigbur et al., 2011; Cohen & Ridderinkhof, 2013; Cohen et al., 2008), which increase top-down cognitive control mechanisms during spatially-incongruent trials to enable the correct response. Recently, conflict-related changes in frontal theta activity were not only found in the Simon-like S-R task but also in the OS-R task (Cao et al., 2017). Whereas the results in the S-R task replicated the theta pattern found by previous studies, frontal theta power increased during the spatially-congruent in comparison to the spatially-incongruent condition in the OS-R task. This is the only study showing that top-down control is mediated by frontal theta synchronization in an OS-R task.

4.1.3 Spatial S-R mapping and alpha band changes

Cohen and Ridderinkhof (2013) also looked at differences in alpha band activity (8-12 Hz) during a Simon paradigm and found more alpha desynchronization in the spatially-incongruent in comparison to spatially-congruent condition in right parietal areas from 600 to 750 ms after stimulus presentation. However, since RTs were typically shorter than 600 ms the alpha power decrease was not related to conflict resolution. Rather it influenced responding on the proceeding trial. Instead, frontal alpha desynchronization has been related to conflict management on spatially-incongruent in comparison to spatially-congruent trials in a Simon-like S-R task (K. Wang, Li, Zheng, Wang, & Liu, 2014). However, since this study only used a single electrode it is difficult to know whether the

alpha activity originated from frontal or more posterior areas. This is important since posterior alpha synchronization inhibits the visual stream, which could be important when withholding the spatially-congruent response during spatially-incongruent trials in an S-R task (Klimesch et al., 2007; Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009; Klimesch, 2012).

On the other hand, alpha desynchronization in posterior regions is associated with increased mental effort, which could be important when handling spatial response-conflict (Sauseng et al., 2005). Since it is more difficult to execute the correct response on spatially-incongruent in comparison to spatially-congruent trials in a Simon-like S-R task, more effort is required for the latter. However, very little studies have actually reported posterior alpha activity during spatial response conflict (Corbetta & Shulman, 2002; Liu, Banich, Jacobson, & Tanabe, 2004; Kerns, 2006). Hence, posterior alpha desynchronization as an indicator for mental effort might not be crucial to overcome spatial response-conflict. In sum, posterior alpha synchronization could either be helpful when inhibiting unwanted responses whilst posterior alpha desynchronization could be important when coping with the increased difficulty during spatial conflict.

4.1.4 Spatial S-R mapping and beta band changes

Although it has repeatedly been shown that sensorimotor beta activity desynchronizes more during response-conflict [18] in comparison to stimulus-conflict [19] (V. Van Veen & Carter, 2005; Zhao et al., 2015), few studies have actually measured beta oscillations during a Simon task, which evokes response-conflict. One study found increased beta desynchronization in the frontal cortex during spatially-incongruent in comparison to spatially-congruent trials in an S-R task (K. Wang et al., 2014). However, since only one frontal electrode (Fz) was used, it is difficult to know whether the changes were centred over frontal areas or whether the effect was mediated by changes in central areas. The latter scenario is very likely since beta band desynchronization in motor areas is neces-

[18] Inconsistency between a learned S-R mapping and a required response
[19] Inconsistency between stimulus characteristics

sary for executing voluntary movements as those required during an S-R task (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013). A second study measured beta band changes during A Stroop task from the subthalamic nucleus [20]. Here beta activity desynchronized on matching and non-matching trials after the presentation of the stimulus. However, in the non-matching condition a slight re-synchronization was found before responding. This temporary re-synchronization was interpreted as inhibition of the response until the conflict was resolved (Brittain et al., 2012). This result is in line with findings showing that a sudden inhibition of a motor output quickly synchronizes the beta frequency (Y. Zhang, Chen, Bressler, & Ding, 2008). No studies have measured beta oscillations during a reversed Simon-like task.

All in all, most research covering the Simon effect has assessed frontal theta activity during the S-R and OS-R tasks and found more synchronization on spatially-incongruent in comparison to spatially-congruent trials in the S-R task and the reversed pattern in the OS-R task. These findings are widely accepted and interpreted as increased top-down control during spatially-incongruent in comparison to spatially-congruent trials in the S-R task and vice versa in the OS-R task. The findings for alpha and beta frequencies are less consistent. Also, no work has been done on the function of alpha and beta frequencies during the S-R mapping in an OS-R task. Hence, the present study was used to gain more insight into the role of alpha and beta frequencies during spatially-congruent and spatially-incongruent trials in a Simon-like task and its reverse, while aiming at replicating the widely accepted conflict-related results in the theta band. Although theta, alpha and beta frequencies were summarized separately and will be analyzed separately it is critical to keep in mind that they do not work in isolation. For example, alpha and beta frequencies often desynchronize together when the cortex is activated (van Wijk, Beek, & Daffertshofer, 2012; Cheyne, 2013), which means that these frequencies are highly correlated (Carlqvist, Nikulin, Strömberg, & Brismar, 2005). Also, frontal theta and parietal

[20]In the Stroop task participants observe colour words (e.g. 'red'), which are displayed in different colours. Participants are asked to name the colouring and disregard the word semantics. On congruent trials the written and coloured information match, whereas it is not matching in the incongruent condition. Hence, the Stroop task evokes stimulus-conflict.

alpha bands are associated during a Simon task, since the frequencies show enhanced coupling on spatially-congruent trials (Cohen & Ridderinkhof, 2013). Hence it is likely that theta, alpha and beta frequencies together form the neural processes guiding SCy effects.

4.1.5 Hypotheses: SCy effects in the bS-R and bOS-R tasks

In the present experiment theta, alpha and beta frequencies are assessed for SCy and reversed R-SCy effects. This is done to examine how the spatially-incongruent cues are inhibited in the bS-R task, and how the spatially-congruent cues are inhibited in the bOS-R task. These insights will provide a thorough understanding of the underlying neural network of spatial S-R mapping, which will be compared to the biological equivalent in the next chapter. This will answer the question whether spatial and biological stimuli are processed in similar neural networks or whether humans have developed a specialized neural network to process of biological cues. Based on the research above it is hypothesized, that the theta band will synchronize more in the spatially-incongruent in comparison to the spatially-congruent condition in the bS-R task and show the opposite effect in the bOS-R task. The hypotheses for alpha and beta bands are less clear. Alpha power in posterior regions could decrease more during the spatially-incongruent in comparison to spatially-congruent condition in the bS-R task, whereas the opposite pattern could be revealed in the bOS-R task. This could be related to the increased mental effort triggered by S-R conflict. However, evidence exists that posterior alpha desynchronization during a Simon task is not related to 'online' conflict resolution but to the behavioral adjustments on the following trial. This will be assessed by correlating the neural results during action preparation with the behavioral SCy and R-SCy effects. Lastly, the beta band could show a momentary re-synchronization during spatial response-conflict, which would indicate a temporary inhibition of the response until the conflict has been resolved.

4.1.6 Neural correlates of conscious imitation and counter-imitation

Although the present study has its focus on automatic imitation and automatic spatial S-R mapping, the current paradigm also incorporates the conscious counterpart to these processes. In the previous behavioral studies conscious imitation was assessed by comparing RTs in the bS-R and bOS-R tasks, since participants had to consciously imitate the movement in the former but performed counter-imitative movements in the latter. Therefore, the following sections will illustrate the neural processes underlying conscious imitation and its beneficial effects on behaviour. As discussed in the General Introduction, conscious imitation could rely on the MN system, which is proposed to facilitate imitation by automatically triggering the observed movements in the observer's motor system (Iacoboni, 2005). Much of the research on conscious imitation has focused on mu activity. As discussed in the General Introduction mu activity shows the same characteristics as MNs. That is, more mu desynchronization is observed when a movement is executed or when the same movement is observed (Gastaut & Bert, 1954). However, whether this means that changes in mu activity is essential for conscious imitation will be reviewed next.

4.1.7 Conscious imitation and mu/alpha activity

Much research on imitation has been done in patients with autistic spectrum disorder (ASD) and aged match controls, since patients with ASD exhibit difficulties with self-other representations due to a 'broken down' MN system (Hobson & Bishop, 2016). For the present introduction, the focus is not on whether the 'broken down MN' theory is correct but on the actual neural response associated with conscious imitation in ASD and controls. Most EEG and MEG studies in the ASD literature assessed the mu rhythm by limiting the data analysis to sensorimotor areas (electrode C3, C4 and Cz). Bernier et al. (Bernier, Dawson, Webb, & Murias, 2007) recorded central mu activity while participants (controls and ASD) imitated observed hand movements and found increased mu rhythm during imitation in comparison to baseline. More interesting, increased mu desynchroniza-

tion predicted better imitation skills. These results were partly replicated in the follow-up experiment (Bernier, Aaronson, & McPartland, 2013), where mu desynchronization during action observation predicted the ability to imitate facial movements. These studies suggest a potential link between central mu rhythm desynchronization and successful imitation. However, these findings have been challenged by other studies, which do not find any relationship between the ability to imitate and the degree of mu desynchronization (Ruysschaert, Warreyn, Wiersema, Oostra, & Roeyers, 2014; Y.-t. Fan, Decety, Yang, Liu, & Cheng, 2010).

Research assessing imitation in a non-clinical setting have used the same approach and only considered mu activity in the sensorimotor cortex. Muthukumaraswamy and Johnson (Muthukumaraswamy & Johnson, 2004) found increased mu desynchronization over the sensorimotor cortex [21] during imitation in comparison to action observation. Further, imitation, observation and movement execution showed very similar topographies of mu desynchronization over sensorimotor cortices. This was interpreted as evidence for an overarching MN system underlying all behaviours.

A more recent study by Désy and Lepage (Désy & Lepage, 2013) also recorded mu desynchronization over averaged central electrodes (electrodes C3, C4 and Cz) during conscious imitation of biological (finger lifts) and non-biological (dots mimicking the movement trajectory of the finger lifts) stimuli. Greater mu desynchronization was found during the imitation of biological movements in comparison to the 'imitation' of non-biological stimuli. Importantly a control electrode over the occipital cortex (Oz) did not show this effect. This meant that central mu desynchronization was not guided by posterior alpha desynchronization but an independent phenomenon especially important during imitation.

Differentiating between conscious imitation and conscious spatial cueing, Kessler et al. (Kessler et al., 2006) identified a frequency band from 6 to 14 Hz, which showed increased power in the spatial condition in comparison to the biological condition. Next

[21] Eight electrodes on each hemisphere located close to C3 and C4.

this band-with (6-14 Hz) was used to examine the peak synchronization rate between areas in the neural networks processing biological or spatial cues. Conscious imitation triggered enhanced activity in a neural network incorporating MNs areas (vPMC and parts of the parietal cortex) before these areas showed enhanced synchronization in the spatial condition. A follow-up study, which assessed ERPs using the same paradigm confirmed the early involvement of the vPMC during biological in comparison to spatial cueing (Biermann-Ruben et al., 2008). Together the studies provide affirming evidence that MN areas are essential for conscious biological imitation.

Importantly, it has been suggested that central mu activity is related to tactile mirroring rather than motor mirroring. Evidence comes from studies assessing central mu desynchronization in a repetition suppression paradigm [22]. If MNs respond to specific actions or tactile information then more repetition suppression (increased mu power) should be observed when exactly the same event is repeated than when the event is slightly altered. However, repetition suppression in the mu band only occurs for tactile and not for motor events, suggesting that tactile information might be more important for mirroring (Coll, Bird, Catmur, & Press, 2015). This result was supported by an additional study, showing that mu desynchronization [23] could not be used to distinguish different types of actions but could reliably predict whether a tactile event was present or not (Coll, Press, Hobson, Catmur, & Bird, 2017).

4.1.8 Conscious imitation and beta activity

While the studies presented above focused on mu or alpha activity, others have taken a more broadband approach. For example, Muthukumaraswamy and Singh (2008) assessed changes in alpha and beta frequencies during the observation of biological stimuli. Depending on the condition participants either remained still, imitated the observed stimuli or performed simple mathematical tasks. In the two latter conditions posterior beta desynchronized more than during the pure observation condition. No difference in beta

[22] The reduction of neural activity when a behavior is repeated
[23] In the beta band

desynchronization was found between the imitation and arithmetic conditions. This led to the conclusion that changes in posterior beta activity during the observation of biological stimuli was influenced by mental effort. This raises the question how it is possible to discern beta desynchronization related to mental effort and S-R mapping during imitation (Gola et al., 2013; Siegel et al., 2008).

Whereas most MEG or EEG studies have focused on specific areas to find neural evidence for S-R mapping during imitation, fMRI research have found more widespread brain networks related to imitation. For example, Mengotti, Dell'Acqua and Rumiati (Mengotti et al., 2012) used a similar paradigm as in the present studies whilst recording fMRI. They found that the biological task (bS-R and bOS-R tasks) in comparison to the spatial task (sS-R and sOS-R tasks) activated MN areas such as the IFG, the IPL and the superior parietal lobule (SPL) but also additional areas such as the central gyri and the occipital cortex. No differentiation was made between the bS-R and bOS-R tasks and, therefore, the differences between conscious imitation and counter-imitation were not assessed. Another fMRI study has revealed that delayed imitation [24] activated MN areas such as the IPL and the IFG (Buccino et al., 2004). These results provide evidence that MN areas in frontal and parietal cortices may form a specialized brain network, which processes biological stimuli.

These insights are in line with the direct-matching model of (Sauser & Billard, 2006), which suggests that biological but not spatial stimuli are processed in a direct S-R matching pathway that incorporates MN areas such as the vPMC. In contrast, non-biological stimuli are processed in the PPC, which receives top-down modulating input from the PFC to adapt the S-R mapping to the task instructions. This is in line with the observation that non-biological stimuli trigger more frontal theta synchronization than the observation of biological stimuli. This suggests that the recognition of non-biological in comparison to biological stimuli require more top-down control processes, since more effort is required to relate the perceived stimuli to pre-existing memories (Urgen et al.,

[24]Movement observation with delayed movement repetition.

2013).

All In all, evidence exists that conscious imitation engages MN areas. This can be assessed by central mu and alpha activities. On the other hand, posterior beta band changes during imitation are likely related to mental effort and thus difficult to distinguish from cognitive processes related to S-R mapping. Unfortunately, most MEG an EEG studies have not assessed brain networks during imitation and, hence, were not able to replicate the MN networks found in fMRI studies during imitation. The following studies will fill this gap by examining whether theta, alpha and beta frequencies can help us to understand the complexity of the human MN network.

4.1.9 Execution – observation paradigms and imitation

The execution-observation paradigm was first used to assess MN activity in macaque monkeys as described in the General Introduction. Since these studies only require the participants to observe or execute an action, imitation is not directly part of the paradigm. It is instead linked indirectly since the observation of actions triggers covert imitation in the observer's motor system (Vannuscorps & Caramazza, 2016).

This idea has been supported by TMS experiments (Fadiga et al., 1995; Catmur et al., 2007; Enticott et al., 2010) described in the General Introduction, which have shown that observing a movement activates the observer's motor system and, therefore, facilitates the execution of the same movement. However, since such facilitation effects have been observed when non-biological stimuli are presented as well, these conclusion have been debated. (Petroni et al., 2010).

Importantly, during observation-execution paradigms participants are not unconsciously introduced to the biological stimuli but consciously observe or execute an action. Due to this reason execution-observation studies are summarized here and not when discussing automatic imitation in the following Chapter.

In execution-observation studies, mu activity has often been measured while participants observe and perform movements (Gastaut & Bert, 1954; Pineda, Allison, & Vankov,

2000; Pineda, 2005; Oberman, Pineda, & Ramachandran, 2007). One study measured mu activity as well as fMRI BOLD responses while participants executed and observed actions and found mu desynchronization in MN areas (IPL and PMC) in both conditions. Further, this activity was correlated with the BOLD response, which is an indicator for brain activity. Therefore, the study provided convincing evidence that action observation activates similar areas as action execution and that such mirroring mechanisms can be measured by mu desynchronization in MN areas (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). Other studies have measured alpha and beta frequencies during action execution-observation paradigms and found that both alpha and beta bands desynchronize in the same MN areas (e.g. IPL, IFG, vPMC) during the execution and observation of actions (Sebastiani et al., 2014; Babiloni et al., 2002). Hence, alpha and beta frequencies can be used to assess which brain areas could be involved in mirroring. However, since no comparison between biological and spatial cues were included in these studies, the results do not indicate whether mirroring mechanisms are unique to biological stimuli.

fMRI studies instead have compared the neural activity during the observation of biological or non-biological moving stimuli with the neural signature during action execution, by showing human and robotic movements. In one study, only the observation of human movements activated MN areas (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). However, a follow-up study revealed that this difference between human and robotic stimuli only occurred when the same robotic movement was repeated during the one experimental block (Gazzola, Rizzolatti, Wicker, & Keysers, 2007).

In conclusion, action execution-observation studies measuring neural oscillations have found evidence that mu, alpha and beta activity can be used to assess human mirroring in areas belonging to the core MN network discovered macaque monkeys (Molenberghs et al., 2012; Kilner & Lemon, 2013). However, future MEG and EEG studies are required to replicate the findings from fMRI research, to assess the complex time-frequency signatures, which accompany the processing of biological and non-biological stimuli.

4.1.10 Hypotheses: conscious imitation and counter-imitation

In the present experiment theta, alpha and beta frequencies will be assessed for conscious imitation and counter-imitation, by comparing neural activity during action preparation with neural activity during a baseline in the bS-R and bOS-R tasks separately. This is done to assess whether conscious imitation uniquely elicits MN activity. The results will be of interest when comparing conscious imitation with conscious spatial cueing to observe the differences in the underlying neural networks. Based on the research above, it is hypothesized that the alpha, mu and beta activities will show increased desynchronization in the classical MN system (the IFG, vPMC and IPL) during conscious imitation (bS-R task). If the observed effects are due to mirroring, they should not be replicated during counter-imitation (bOS-R task), since this behavior should counteract mirroring. Since studies assessing conscious mirroring have focused on alpha and beta frequencies, the present study is the first, which also examines the potential role of theta oscillations during conscious S-R mapping. However, evidence exists that frontal theta synchronization is evoked less when a stimulus is familiar (Urgen et al., 2013). Therefore, it is likely that no frontal theta will be observed when using highly familiar biological stimuli such as hands. The present experiment repeated the mixed bS-R and bOS-R tasks described in Chapter 2 whilst recording MEG data to assess the neural correlates associated with spatial S-R mapping and conscious imitation.

4.2 Methods - Experiment 5

4.2.1 Participants

24 participants took part in the experiment (males = 12 , mean age = 29, sd=4). Three participants were excluded since they made too many errors. All experimental procedures complied with the Declaration of Helsinki and were approved by the Aston University, Department of Life and Health Sciences ethics committee. Participants gave written informed consent before participating in the study.

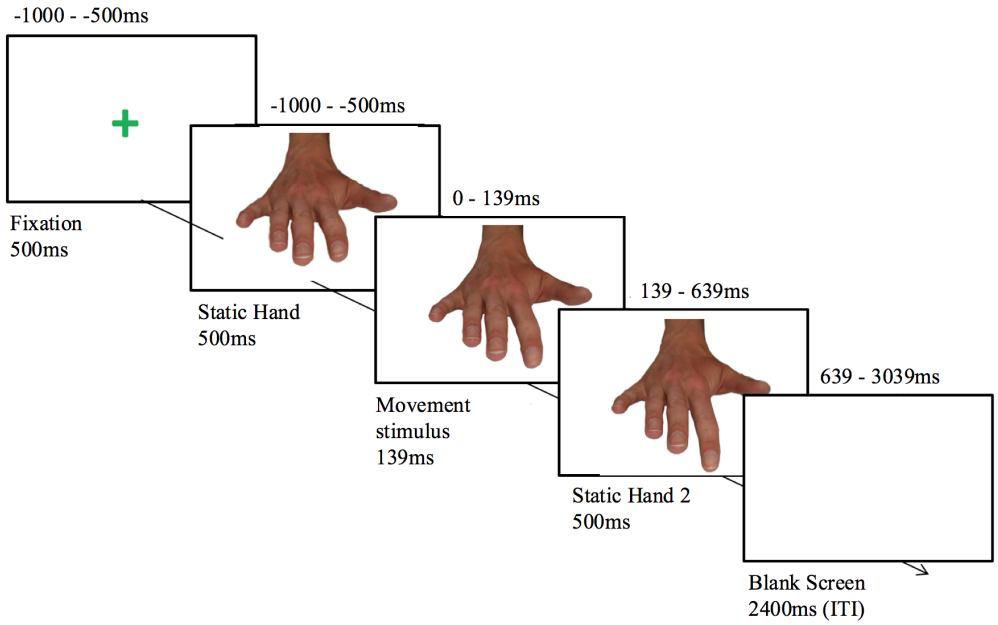


Figure 20: Shows the procedure for the bS-R and bOS-R tasks of Experiment 5. A trial starts with the onset of the coloured fixation cross, which indicates to perform the bS-R or bOS-R task. Next a static hand appears on the screen (500 ms), which performs a tapping movement with the index or middle finger (139 ms). The hand stays on the screen for 500 ms in the final position before a blank screen appears (2400 ms). In the sS-R and sOS-R tasks the same procedure was used but the inter-trial interval was shortened to 1872 ms since the RTs were shorter than in the bS-R and bOS-R tasks.

4.2.2 Materials and procedure

Figure 20 shows the procedure of the current experiment. In general, the experiment was very similar to Experiment 4 with a few alterations. Again, the stimuli from Boyer et al.

(2012) were taken as the starting point for creating four movies, each beginning with the presentation of an image of a right or left hand viewed from a third person perspective. Different from the prior experiments, the hand initially remained static for 500 ms before it performed a downward tapping movement with either the middle or index finger. This movement again acted as the imperative stimulus and was split into eight frames (16.7 ms each) for a total duration of 133.3 ms. At the end of the movement the finger remained in the downward position for further 500 ms. In total the hand image was shown for 1233 ms and in between stimuli, a blank, white screen appeared for 2400 ms to allow the beta rebound to reach baseline before the next trial started. In contrast, to Experiment 2, no coloured frame was presented to indicate the to be performed task. Instead, a blue or green fixation cross was presented for 500 ms (Psychophysics Toolbox text size 40, 3*3cm, 1.99°) before the presentation of the first static hand. The colour of the fixation cross prompted the participants to perform the bS-R or bOS-R task as soon as the imperative stimulus did a tapping movement. In the original position, the displayed hand had a horizontal visual angle of 10.92°and a vertical visual angle of 13.42°. While the hand remained in this position during the whole trial the active finger performed a downward movement of 30°. The stimuli were programmed and controlled using Psychophysics Toolbox (PTB-3) and MATLAB 2012b (The MathWorks, Inc., Natick, Massachusetts, United States) software.

The experiment consisted of 368 trials split equally across the bS-R and bOS-R tasks. This lead to 92 trials per condition (Task*Congruency). Note, that the first five participants performed 328 trials (82 trials per condition). The number of trials were increased after 5 participants to make sure that 60 trials were kept for the analysis after trials with erroneous or too slow responses were discarded. Before starting the experiment verbal instructions were given and 15 practice trials were administered.

4.2.3 Apparatus

MEG recording: A Neuromag MEG system (Vectorview, Elekta, Finland) with 306 channels (204 gradiometers and 102 magnetometers) acquired data with a sampling rate of 1000 Hz in a magnetically shielded chamber. Before the recording, five head position indicators (HPI) were positioned on the mastoid bones and on the forehead to measure the head position during the scanning period. Head position changes were assessed using Elekta Maxfilter software. Three fiducial coordinates (nasion, left ear, right ear) and approximately 600 scalp coordinates were also acquired by the use of the Polhemus Fastrak digitizer for the coregistration of the individuals MEG data and MRI T1 image.

Experimental set-up: Participants were seated in the chair of the Elekta Neuromag scanner (68°sitting position) 86 cm away from a projector screen on which the visual stimuli were presented. A response box with two response buttons were placed in front of the participants. Participants positioned the middle and the index finger of their right hand on separate response buttons. Responses from the participants were captured by the acquisition software from Elekta Neuromag. The critical time stamps from the experiment was transferred to the Elekta Neuromag software using a LabJack U3. To ensure correct timing a photodiode was placed at the right bottom corner of the projector screen and connected as an analogue input to the Neuromag data acquisition software.

MRI scan: A structural T1 brain scan was acquired using a Siemens MAGNETOM Trio 3T scanner incorporating a 32-channel head coil. The T1 scan had to following parameters: voxel-size = 8 8 8 mm, TE = 2.18 ms, TI = 1,100 ms, TR = 2,300 ms, flip angle = 9,192 and 208 slices.

Coregistration: The headshape of the individuals MRI was segmented using the Neuromag Elekta software (segmentationlab). Matlab 2014b was used to coregister the individual T1 scan with the MEG head position using the fiducial coordinates and the head surface information from the Polhemus Fastrak digitizer. Fieldtrip toolbox v20161024 (Oostenveld, Fries, Maris, & Schoffelen, 2011) was used to segment the MRI into different brain tissue (brain, skull and scalp) and the same toolbox was used to create the single-

shell volume conductor (Nolte, 2003) with the inner skull as boundary, which was needed to calculate the forward and inward models during the source analyses. The mesh was set to 8 mm per voxel.

4.2.4 Pre-processing

MEG data was pre-processed using Maxfilter (temporal signal space separation: tsss, .98 correlation), which suppresses external sources by applying spatial filtering and suppresses internal but irrelevant sources by applying statistical methods, which takes the time domain into account (Taulu & Simola, 2006). The data was saved in two different datasets, since the recording time exceeding the capacity of the in-house system. The two datasets needed to be cleaned separately using Maxfilter (tsss). Maxfilter separates the data into components however, the number of components can be different between datasets especially if these differ in length. Further pre-processing was performed in Matlab 2014b using the open-source Field- trip toolbox v20161024 (Oostenveld et al., 2011). A bandpass filter (0.5 Hz to 90 Hz) and a bandstop filter (47 Hz - 53 Hz) was applied to the data to remove line noise and high frequency muscles artefacts. The data was epoched into trials where zero was the onset of the tapping movement on the screen. Each trial started from onset of the fixation cross and ended with the offset of the inter-trial-interval (ITI) but additional 500 ms were added at the beginning and the end of the trial to avoid artifacts during the frequency analysis.

The trials were visually inspected to remove noisy channels or trials due to internal (e.g. eye blinks, muscles tension) or external artifacts (e.g. squid jumps). If any eye or heart artifacts remained in the data, these were identified by an independent component analysis and removed from the data (Vigário, Jousmäki, Hämäläinen, Hari, & Oja, 1998). MEG channels that were noisy prior to acquisition were interpolated for the sensor level analysis and removed from the source level analysis.

Only gradiometers were used for the analysis, since the differences in scaling between magnetometers and gradiometers distorted the data. For the sensor level analysis the 204

gradiometers were combined to 102 planar gradients. Lastly the datasets for each subject was concatenated and the co-variance matrix was adjusted so that the whole dataset was explained by the same amount of components.

4.2.5 Sensor analysis

The sensor analysis was performed in Matlab 2014b using the open-source Fieldtrip toolbox v20161024 (Oostenveld et al., 2011). The time frequency analysis was done on the entire epoched data from -1500 ms before stimulus movement onset until 3300 ms after stimulus movement onset, using a hanning taper with 3 frequency cycles per time window. The analysis was done in steps of 1 Hz and a sliding window of 20 ms.

In general, two distinct analyses were performed: In a between-conditions analysis the neural activity during action preparation between congruent and incongruent conditions. For this analysis a relative baseline from -1000 to -700 ms was applied when plotting the data. For the statistical analysis no baseline was used, since the trials were randomized and no constant deviation between conditions was expected. Secondly, a within condition analysis was run, which compared a baseline period (this will be referred to as rest period) to a action preparation period. For this analysis the action preparation period (50 ms to 500 ms) was plotted with a relative baseline that corresponded to the rest period (-500 to -50 ms).

The frequency bands used for the analysis were theta 4-7 Hz; alpha, 8-12 Hz and beta 13-25 Hz. These frequency bands are based on the frequency bands used in the literature summarized in the Introductions of Experiment 5 and 6 (Sebastiani et al., 2014; Babiloni et al., 2002; Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). Significance testing was performed by means of a cluster based permutation test. Here, the power of each channel is subtracted between conditions and the value is quantified by means of a t-value. A channel is kept for further analysis if the p-value of the specified t-value is smaller than the specified cluster alpha ($p<0.05$). The resulting channels are grouped based on temporal, spatial or spectral characteristics and the significant t-values of all grouped channels are

summed. The resulting value is used to calculate the test statistic for the clusters using the montecarlo method. In the sensor level test, this results in a distinct p-value for each 20 ms (Maris & Oostenveld, 2007).

4.2.6 Source analysis

For the source analysis a sourcemodel was warped to mni space using a template grid from the the Fieldtrip toolbox with 8 mm diameter. The leadfield was normalized in order to prevent the power bias to the center of the head. The source analysis was conducted using a Dynamic Imaging of Coherent Sources (DICS) beamformer (Gross et al., 2001). The DICS is a source analysis, which applies a linear spatial filter that adds a constant (a unit gain) to the voxels, which are assessed, while suppressing the surrounding voxels. It employs the cross spectral density matrix, which contains the Fourier transformed cross correlations of the frequency of interest from two different sources. If the source is correlated with itself the power of the source can be estimated, which is used in the source analysis in the current study. Together with the information of the forward model it produces a reliable estimate of the activity in a given voxel. The DICS beamformer is based on calculations in the frequency domain. Therefore, a time frequency analysis with a hanning taper was re-run for each specific frequency band separately for each beamformer. For the source analysis the conditions were added to create a common filter, the regulation parameter lambda was set to 5 percent and only the largest of the three dipole directions per spatial filter was used for the calculations.

The statistical analysis used two tailed cluster based permutation tests (montecarlo) with a cluster alpha of 5 percent and 5000 permutations. As in the sensor level cluster permutation tests, the source level test uses the averaged power over a pre-specified period. Based on the frequency band the time period was adjusted to include a minimum of two to three frequency cycles to enable a sufficient frequency resolution without sacrificing the temporal resolution. In Simon-like paradigms, theta, alpha and beta bands have been studied using <= 400 ms, 300 ms and 300 ms respectively (Cohen & Cavanagh, 2011;

Cohen & Ridderinkhof, 2013). Therefore, these time windows were taken as minimum for the theta, alpha and beta bands. However, if possible the time windows were increased to allow greater frequency resolution. The results of the test statistics were visualized by plotting the significant t-values on an interpolated MRI. Anatomical automatic labelling was used to visualize the affected MNI coordinates and the corresponding brain labels (Tzourio-Mazoyer et al., 2002).

4.2.7 Virtual electrode

A virtual electrode was placed in the local mimina/maxima in the revealed clusters. This was done using a Linearly Constrained Minimum Variance (LCMV) beamformer (B. D. Van Veen, Van Drongelen, Yuchtman, & Suzuki, 1997). This is similar to the DICS beamformer with the important difference that no Fourier transform is used. A Fourier transform creates a complex filter and loses the time information. Instead, the LCMV beamformer calculates the power of the frequency of interest over time. A time frequency analysis was calculated in steps of 1 Hz, with a hanning taper, a time window, which included three cycles per frequency and a sliding window of 10 ms. The difference between-conditions (congruent vs incongruent) or action preparation and rest periods were calculated for each participant separately. This was done by subtracting the output from the congruent condition from the output of the incongruent condition or by subtracting the output from the rest period from the action preparation period. As in the sensor level frequency analysis, a relative baseline between -1000 ms to -700 ms was used when plotting the results from the between-condition analysis (incongruent-congruent). In the within condition analysis the rest period functioned as a relative baseline to the action preparation period. Statistical permutation testing on the virtual electrode data was only performed on the between-condition data, since these results were correlated with the behavioural congruency effects (see next paragraph). In the permutation test the averaged theta, alpha or beta frequency was compared between conditions (incongruent – congruent condition) over time with no baseline applied. The time window used for the

test statistic corresponded to the time window defined in the section below: 'Choosing the time period of interest'[25]. The test was corrected for multiple comparison using the false discovery rate.

4.2.8 Correlation between behavioral and MEG data

To assess whether the activity in the sources significantly correlated with the behavioral congruency effects, the power differences between conditions of the virtual electrode was correlated with the behavioral congruency effect. This was done to estimate whether the differences in desynchronization/synchronization between conditions could predict the difference in RTs between conditions. The frequency band, that revealed the significant source was used for the correlation.

From the significant time period of the virtual electrode the power values of the difference between conditions (incongruent-congruent condition) were averaged for each participant. Next, the results were correlated with the difference in reaction times between conditions (incongruent- congruent condition). Each data point in the correlation would therefore represent one participant. Outliers in the behavioral data or the virtual electrode data were removed based on three standard deviations above or below the mean. Next Cooks' D was measured to discover values in the linear regression, which deviated from the general trend in the sample. If the values were equal to or larger than 4/N, the values were removed. Next the variables were tested for normality and homoscedasticity by means of the Shapiro Wilks' test and the Whites test. If both criteria were met the Pearson correlation could be used. If not, the Spearman correlation was used.

4.2.9 Analysis of the behavioral data

The analysis of the behavioral data was identical to the analysis described in Chapter 2. In this experiment, the influence of TASK (bS-R/bOS-R) and spatial CONGRUENCY (spatially-congruent/spatially-incongruent) on RTs and errors rates were analyzed. No

[25]In a few cases this time window was extended based on insights from the sensor level analysis. In such cases the applied time window will be pointed out in the specific paragraphs in the result section.

quintile (delta plots) or variance testing was applied.

4.2.10 Choosing the time period of interest

In general, the present study was set-up to assess the neural activity during action preparation when SCy effects were triggered. Therefore, the lower cut-off of the analysis period was the onset of the observed tapping movement, since this prompted the participants to react. The upper cut-off was the mean reaction time of the fifth reaction time quintile. This corresponded to 700 ms in the bS-R task and 800 ms in the bOS-R task. Within the period from 0 to 700/800 ms the time of the source and sensor level analysis was adjusted depending on the frequency (theta, alpha and beta band) and the time-frequency pattern observed in the sensor level plots.

The median RT was not used as a higher cut-off, since this would disregard half of the responses, which would be ongoing by the time of the cut-off. This could decrease the signal to noise ratio in the data. A higher cut-off, on the other hand, would increase the likelihood to incorporate post-response brain mechanisms into the analysis. This trade-off is balanced by separating between effects that start during later time periods from effects, which start relatively early but continue to evolve during later time periods. In the former case, the likelihood is larger that it is a post-response mechanism. However, in the latter case the activity pattern could represent a response preparation effect, which accumulates over time.

4.3 Results - Experiment 5

4.3.1 Behavioural results

Response times from the bS-R task and bOS-R tasks are shown in Figure 21A. The repeated measures ANOVA with TASK (bS-R/bOS-R) and spatial CONGRUENCY (spatially-congruent/spatially-incongruent) as factors revealed a significant main effect of TASK, $F(1,20)=147.22$, $p<0.001$, $\eta^2= 0.88$. Participants reacted faster in the bS-R task in comparison to bOS-R task (478 ± 80 ms vs 614 ± 104 ms, $p<0.001$). A significant main effect of spatial CONGRUENCY, $F(1,20)=17.45$, $p<0.001$, $\eta^2 = 0.46$, indicated that responses on spatially-incongruent trials were faster than responses on spatially-congruent trials (534 ± 81 ms vs 557 ± 140 ms, $p<0.001$). A TASK x CONGRUENCY interaction, $F(1,20)=58.16$, $p<0.001$, $\eta^2 = 0.74$, revealed that participants responded faster on spatially-congruent trials in comparison to spatially-incongruent trials in the bS-R task (451 ± 84 ms vs 505 ± 66 ms, $p<0.001$) but faster on spatially-incongruent trials in comparison to spatially-congruent trials in the bO-SR task (664 ± 98 ms vs 563 ± 84 ms, $p<0.001$). These results replicated the behavioural results found in Experiment 1 and 2.

Error rates from the bS-R and bOS-R tasks are shown in Figure 21B. The repeated measures ANOVA with TASK (bS-R / bOS-R) and spatial CONGRUENCY (spatially-congruent / spatially-incongruent) as factors revealed a significant main effect of TASK, $F(1,20)=22.57$, $p<0.001$,$\eta^2=0.53$. Participants had fewer errors in the bS-R task in comparison to bOS-R task (4.6 ± 2.9 % vs 8.9 ± 7.7 %, $p<0.001$). A significant main effect of spatial CONGRUENCY, $F(1,20)=22.97$, $p<0.001$,$\eta^2=0.53$, indicated that responses on spatially-incongruent trials were less error-prone than responses on spatially-congruent trials (4.7 ± 3.3 % vs 8.8 ± 7.6 %, $p<0.001$). A TASK x spatial CONGRUENCY interaction, $F(1,20)=30.62$, $p<0.001$, $\eta^2=0.61$, revealed that participants made fewer errors on spatially-congruent trials in comparison to spatially-incongruent trials in the bS-R task (4.1 ± 2.5 % vs 5 ± 3.3 %, $p=0.51$). However, this effect was only borderline significant. In the bOS-R task participants made more errors in the spatially-congruent in comparison

to spatially-incongruent condition (13.5 ± 8.1 % vs 4.4 ± 3.3 %, p<0.001).

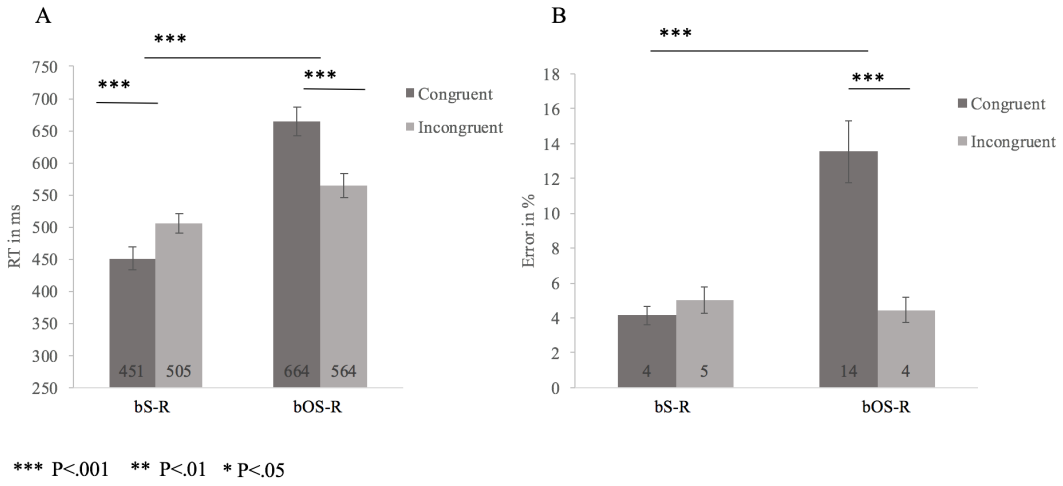


Figure 21: Shows the RTs and error rates in the bS-R and bOS-R tasks. (A) Participants reacted faster in the bS-R than in the bOS-R task. In the bS-R task RTs were faster in the spatially-congruent in comparison to spatially-incongruent condition. This was reversed in the bOS-R task. (B) More errors were made in the bOS-R task in comparison to the bS-R task. In the bOS-R task more errors were made in the spatially-congruent condition in comparison to the spatially-incongruent condition.

	Theta band	Alpha band	Beta band
bS-R task	Significantly more theta desynchornization in the spatially congruent in comparison to spatially incongruent condition in the right S1, left M1 and medial SMA between 200-700 ms.	(1) Significantly more alpha desynchronization in the spatially incongruent condition in comparison to spatially congruent condition in the left CN and left FG between 0-300 ms. Significant negative correlation between the difference in alpha desynchronization between conditions and the behavioural congruency effect: the larger the difference in alpha desynchronization between the spatially incongruent and spatially congruent conditions the larger the behavioral SCy effect. (2) Significant more alpha desynchronization in the spatially incongruent condition in comparison to the spatially congruent condition in the bilateral LG and the right SPL between 400-700 ms	
bOS-R task		No significant effect but a trend showing increased posterior alpha desynchronization in the spatially congruent in comparison to spatially incongruent condition.	No significant effect but a general trend which showed increased posterior alpha desynchronization in the spatially congruent in comparison to spatially incongruent condition.
sS-R task	No significant effects but a tendency of more theta synchronization in the biologically congruent in comparison to biologically incongruent condition in the left S1 and left M1 between 0-500 ms.	(1) Significantly more alpha desynchronization in the biologically incongruent condition in comparison to the biologically congruent condition in the right V1, left LG and left AG between 280 to 800 ms. (2) Significant positive correlation between the difference in alpha desynchronization between conditions and the behavioural BCy effect: a larger difference in desynchronization between conditions is associated with a smaller behavioral BCy effect.	Significantly more beta desynchronization in the biologically incongruent condition in comparison to the biologically congruent condition in the left MFG, FEF, PO and SMG between 280-600 ms. Significant negative correlation between the difference in beta desynchronization between conditions and the behavioural BCy effect: a larger difference in beta band desynchronization between conditions is associated with a larger behavioural BCy effect.
sOS-R task		No significant effect but a general trend showing increased posterior alpha desynchronization in the biologically congruent in comparison to biologically incongruent condition.	Significantly more beta desynchronization in the biologically congruent condition in comparison to the biologically incongruent condition in the in the left VAA, left SPL and left S1 between 300 to 800. The virtual electrode indicated that this effect likely occurred after responding.

Figure 22: Summary of the between condition MEG Results in Experiment 5 and 6.

4.3.2 MEG Results

Having repeated the behavioral results from Experiment 1 and 2 the MEG analysis was used to find neural evidence that spatial stimuli are processed outside MN areas. According to the single and direct-matching models (Sauser & Billard, 2006), S-R mapping of task irrelevant spatial stimuli occurs in the PPC. Hence, one should observe distinctive neural activation in the PPC when task irrelevant spatial stimuli are beneficial for responding (bS-R task congruent condition) and when they need to be inhibited (bS-R task incongruent condition). However, this neural pattern should be reversed in the bOS-R task signalizing that logical recoding has occurred on a neural level. Oscillations in the theta, alpha and beta bands were compared during spatially congruent and spatially incongruent trials. Here the significant results, which help to answer the research questions are shown. For additional results see Appendix D and for a summary of the results in the between condition analysis in the bS-R and bOS-R tasks see Figure 22

The effects of spatial congruency in the theta band : Figure 23A shows the topoplots depicting the difference in the theta band (4-7 hz) between the spatially-congruent and spatially-incongruent conditions (incongruent-congruent condition) in the bS-R task. From here early theta desynchronization in left central channels is observed, which synchronizes after 300 ms. Left central channels were chosen to assess whether the timings of the theta synchronization would fit to temporal pattern of the frontal theta changes observed during response conflict (Cohen at al. 2008). The corresponding difference TFR (incongruent-congruent condition) showed theta desynchronizes between 0 to 500 ms after stimulus movement onset and theta synchronizes from 500 ms after stimulus movement onset (Figure 23B). For statistical testing in the theta band a time window of 750 ms was necessary to incorporate 3 frequency cycles of the lowest frequency (4 Hz). Using a 750 ms time window provided a poor temporal resolution for the current task. Especially since the time-frequency pattern is very transient. Hence, it is important to balance the temporal resolution and the frequency resolution to get the most meaningful results. Based on the time window chosen in the section above (See, Methods - Ex-

periment 5 'Time windows of interest'), a sensor level permutation test from 0 to 700 ms was calculated (incongruent-congruent condition). It revealed a significant positive cluster from 540 to 700 ms in central channels ($p < 0.05$). This relatively late onset of the significant difference in synchronization between conditions, did not fit to the pattern in the topoplots, which showed clear difference in frontal theta synchronization from 350 ms after movement stimulus onset. Theta activity during response conflict are mostly localized using time windows around or shorter than 500 ms (Cohen & Ridderinkhof, 2013; Nigbur et al., 2011). Therefore, the frontal theta (4-7 Hz) differences between conditions (incongruent – congruent condition) was further examined via a beamformer from 200 ms to 700 ms. It showed a significant positive cluster ($p < 0.05$) with the global maximum in the right primary sensory cortex (S1; MNI 12 -36 62) and local maxima in the medial SMA (MNI 0 -12 60) and left M1 (MNI -6 -30 75; Figure 23C). According to the literature theta frequency modulation during spatial conflict should be observed in the pre-SMA/SMA (Cohen and Ridderinkhof, 2013). However, the present source is most prominent in more posterior areas. This raises the question whether the identified source is related to the conflict induced theta activity presented in the literature or whether it represents a different mechanism. A virtual electrode placed in the right S1 (global maximum) showed theta desynchronization in both conditions after the onset of the static hand (Figure 23D). At stimulus movement onset the theta band re-synchronization was higher in the spatially-incongruent than in the spatially-congruent condition throughout the period of the beamformer (200 to 700 ms). For the correlation with the behavioural SCy effect statistical testing was applied to the virtual electrode data to select the precise time period during which the two conditions significantly differed. This revealed that theta re-synchronization was significantly higher in the spatially-incongruent condition in comparison to spatially-congruent condition between 280 and 660 ms ($p<0.05$, See Appendix D Figure 38). However, no significant correlation between the difference in theta synchronization between conditions and the behavioural SCy effect was revealed ($r = -0.04$, $p > 0.05$). These results confirm that spatial conflict is associated with increased

theta activity in medial areas shortly before responding (Cohen & Ridderinkhof, 2013; Nigbur et al., 2011). However, the strength of this effect is not related to the behavioral SCy effect.

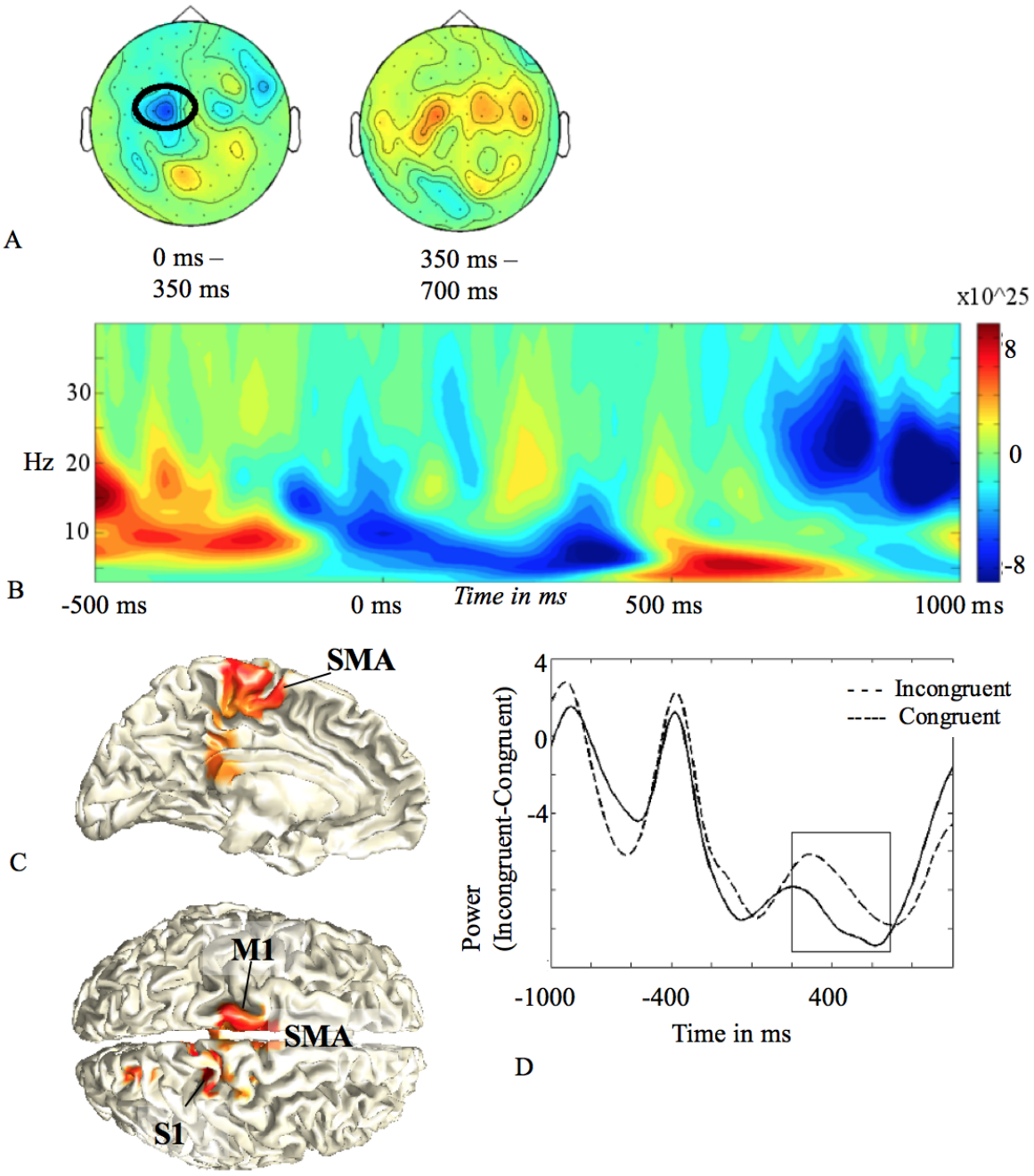


Figure 23: Shows the results of the differences in the theta band activity between spatially-incongruent and spatially-congruent trials in the bS-R task. (A) Topoplots of the differences between conditions (incongruent-congruent condition) in the theta band from 0 to 350 ms and from 350 to 700 ms. The black circle indicates the channels used for the difference TFR shown in B. (B) A difference TFR (incongruent-congruent conditions) from left central anterior channels with a relative baseline between -1000 ms to -700 ms. (C) Source level cluster from 200 to 700 ms locating the difference between spatially-congruent and spatially-incongruent conditions (incongruent-congruent conditions) in the theta band, which shows a positive cluster in the right S1, left M1 and medial SMA.(D) A virtual electrode located in the S1. The virtual electrode depicts the averaged theta power over time with a relative baseline from -1000 to -700 ms. The rectangle indicates the time of the beamformer.

The effects of spatial congruency in the alpha band : Figure 24A shows the topoplots of the differences between the spatially-congruent and spatially-incongruent conditions in alpha band (8-12 Hz). These revealed a negative cluster in left posterior channels throughout the depicted period (0 to 700 ms). This was due to enhanced posterior alpha desynchronization in the spatially-incongruent in comparison to spatially-congruent condition. The corresponding difference TFR showed desynchronization in the alpha band from 0 to 300 ms and from 400 to 700 ms (Figure 24B). However, no sensor level permutation test (8-12 Hz) revealed a significant effect although many different time periods were analyzed (e.g. a sensor level permutation tests from 0-700 ms, 0-500 ms, 0-400 ms, 0-300 ms and 200-700 ms). Due to the posterior alpha signature in the TFR from 0 to 300 ms and from 400 to 700 ms two beamformers were used to reveal potential source level effects. In a Simon-like paradigm alpha frequency has been localized previously using a 300 ms time window (Cohen and Ridderinkhof, 2013). This again shows that the effects in a Simon-like S-R tasks are transient and fast paced. The beamformer (incongruent-congruent condition) from 0 to 300 ms revealed a significant negative cluster with a clear global minimum in left caudate nucleus (CN; MNI -6 12 0) and a local minimum in the left FG (MNI -48 -54 -6; Figure 24C). A virtual electrode was placed into the global minimum corresponding to the left CN and and the average power of the alpha-band activity was calculated for the spatially-congruent and spatially-incongruent conditions. The average power of the virtual electrode in this region (Figure 24D) showed enhanced alpha band desynchronization in the spatially-incongruent in comparison to the spatially-congruent condition from 0 until 600 ms. For the correlation with the behavioural SCy effect statistical testing was applied to the virtual electrode data to select the precise time period during which the two conditions significantly differed. This revealed that the conditions significantly differed from 80 to 230 ms after the onset of the observed action (See, Appendix D Figure 38). Further, the difference in alpha band desynchronization between conditions and the behavioral SCy effect revealed a borderline significant two-tailed negative correlation ($p = 0.062$ $r=-0.44$, Pearson correlation). That is, the behavioural SCy

effect increased if the left CN desynchronized more in the spatially-incongruent condition in comparison to the spatially-congruent condition (Figure 24E).

Figure 25A shows the source localization (incongruent-congruent condition) of the alpha activity between 400 to 700 ms, which revealed a more posterior cluster with global minima in the right LG (MNI 12 -66 -5) and local minima in the left LG (MNI -30 -72 -12) and left SPL (MNI -18 -66 48; $p<0.05$). Interestingly, this cluster was more similar to the cluster found when contrasting rest and action preparation periods. A virtual electrode was placed at the global minimum (right LG) and different local minima and plotted as the average alpha power for the spatially-congruent and spatially-incongruent conditions over time (Figure 25B). None of these virtual electrodes showed a difference between the spatially-congruent and spatially-incongruent conditions in the predicted direction (increased desynchronization in the spatially-incongruent in comparison to spatially-congruent condition). However, the virtual electrode test statistic from the global minimum (right LG) revealed a significant difference between conditions between 500 to 550 ms ($p<0.05$; Appendix D Figure 38). But a Pearson correlation coefficient revealed that this difference between conditions was not related to the observed behavioural SCy effect ($r = -0.27$, $p>0.05$).

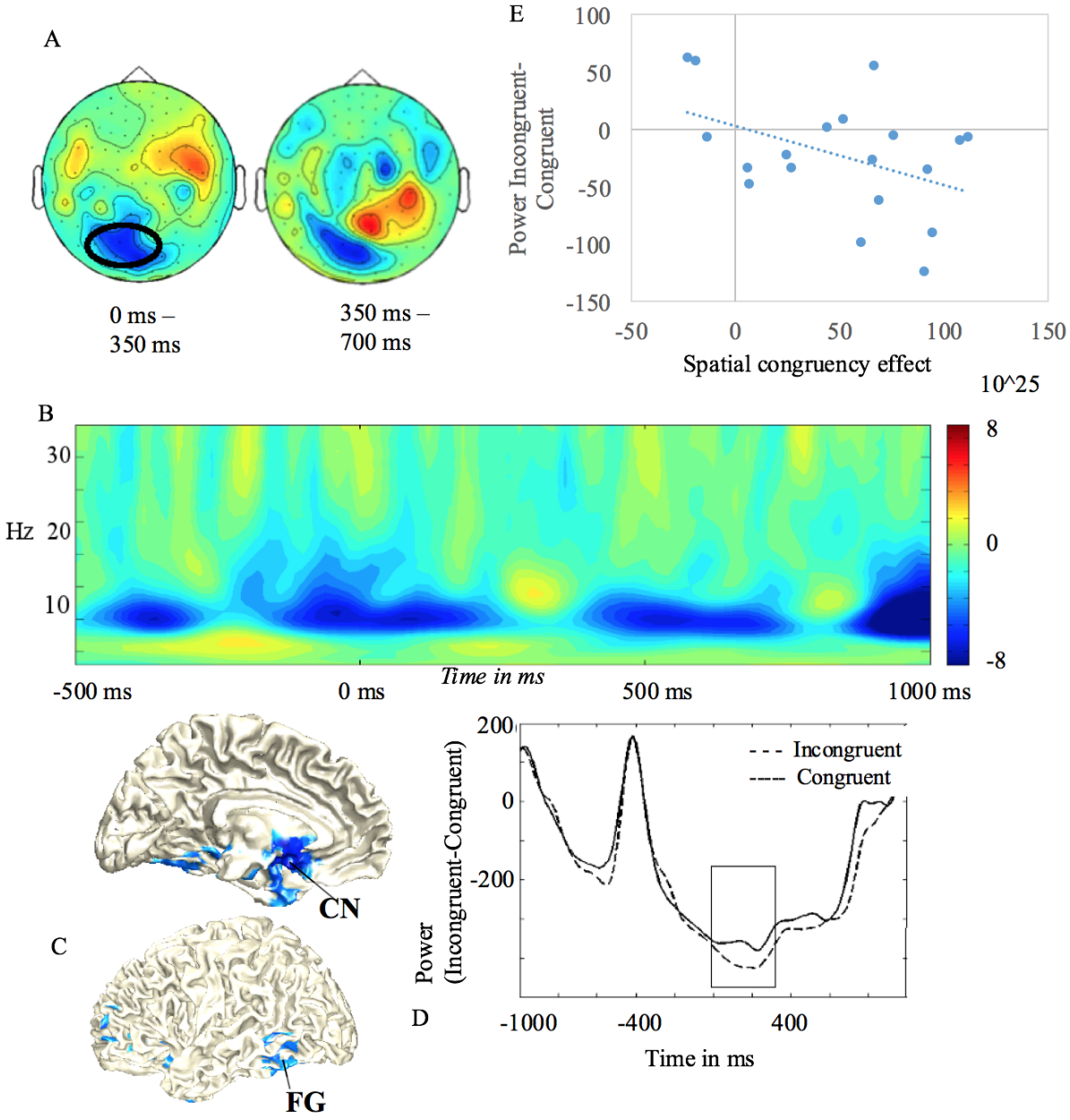


Figure 24: The analysis of the difference in alpha power (8-12 Hz) between spatially-congruent and spatially-incongruent conditions in the bS-R task. (A) Topoplots of the differences between conditions (incongruent - congruent condition) of the alpha band from 0 to 350 ms and from 350 to 700 ms. The black circle indicates the channels used for the sensor level TFR depicted in B. (B) A difference TFR (incongruent-congruent condition) from posterior channels with a relative baseline between -1000 to -700 ms. (C) The output of the source localization (incongruent - congruent condition) in the alpha band from 0 to 300 ms, which shows a negative cluster in the left CN and left FG.(D) A virtual electrode located in the left CN. It shows the averaged power of the alpha band over time with a relative baseline from -1000 to -700 ms in the spatially-congruent and spatially-incongruent conditions. The rectangle corresponds to the time of the beamformer. (E) The correlation of neural and behavioral SCy effect. It shows that the larger the difference in alpha desynchronization between the spatially-incongruent and spatially-congruent conditions the larger the behavioral SCy effect.

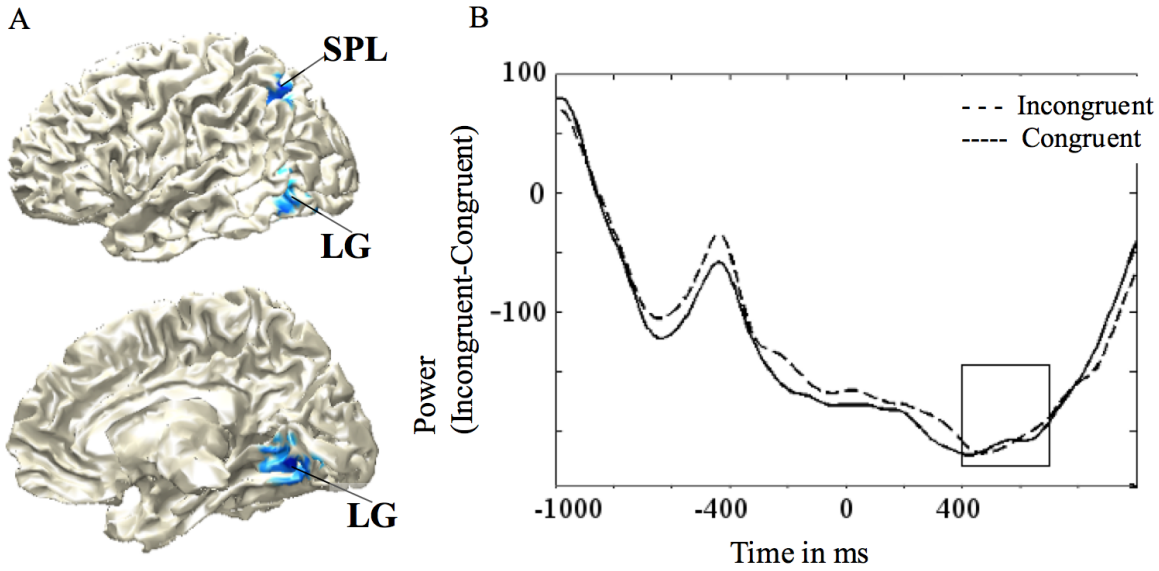


Figure 25: The analysis of the difference in alpha power (8-12 Hz) between spatially-congruent and spatially-incongruent conditions in the bS-R task. (A) The output of the source localization (incongruent - congruent condition) in the alpha band from 400 to 700 ms, which shows a negative cluster in the bilateral LG and the right SPL.(B) A virtual electrode located right LG of the cluster. It shows the averaged power of the alpha band in the spatially-congruent and spatially-incongruent conditions over time with a relative baseline from -1000 to -700 ms. The rectangle corresponds to the time of the beamformer.

The above results examined the neural effects related to the significant behavioural SCy effect in the bS-R task. No significant results were found in the beta band in the bS-R task as well as theta, alpha and beta bands in the bOS-R task. However, especially in the alpha and beta bands there was an opposite tendency compared to the bS-R task so that increased posterior alpha and beta desynchronization was found in the spatially congruent in comparison to the spatially congruent condition. The graphs and corresponding non-significant results are presented in detail in Appendix D.

A second analysis was added, which compared brain activation during the rest period in comparison to the action preparation period to answer the question whether task relevant biological stimuli are processed within the mirror neuron system. However, this analysis provided very broad significant clusters, which could not be discerned from the effects in the analogues analysis for task relevant spatial stimuli in the following chapter. Therefore, the results are presented in the Appendix D. However, for a results summary of the within condition analysis in the bS-R and bOS-R tasks see Figure 26.

	Theta band	Alpha band	Beta band
bS-R task	(1) More theta synchronization in during action preparation in comparison to rest. in the left TP left FPC, left PO, left PFC. (2) More theta desynchronization during action preparation in comparison to rest in the right cerebellum, bilateral LG, bilateral V1 , right VAA, right FG and right AG.	More alpha desynchronization during action preparation in comparison to rest in the right cerebellum, bilateral LG, bilateral AG, bilateral SPL and right FG	More beta desynchronization in the during action preparation in comparison to rest in the left VAA, bilateral SPL, bilateral AG, bilateral cuneus and bilateral V1
bOS-R task	More theta desynchronization during action preparation in comparison to rest in the right cerebellum, bilateral VAA, right LG and right cuneus.	More alpha desynchronization during action preparation in comparison to rest in the right cerebellum, bilateral LG, bilateral AG, bilateral SPL and right FG	More beta desynchronization in the during action preparation in comparison to rest in the left VAA, bilateral SPL, left cuneus, left S1, right and right MFG.
sS-R task	(1) More theta synchronization in during action preparation in comparison to rest. in the left M1, left PMC, bilateral GR and right MFG (2) More theta desynchronization during action preparation in comparison to rest in the left dorsal PCC, right AG, right cerebellum, right LG, right SPL and left VAA	More alpha desynchronization during action preparation in comparison to rest in the right cerebellum, bilateral LG, bilateral AG, right SPL and left posterior cingulate gyrus	More beta desynchronization in the during action preparation in comparison to rest in the right VAA, left VAA, right PCC, left dorsal PCC, left S1 and left AG
sOS-R task	(1) More theta synchronization in during action preparation in comparison to rest left IFG, left PO and bilateral FPC. Did not reach significance. (2) More theta desynchronization during action preparation in comparison to rest in the right LG, right VAA, right V1and right SPL.	More alpha desynchronization during action preparation in comparison to rest in the right AG, right SPL, right LG and left VAA.	More beta desynchronization in the during action preparation in comparison to rest in the left S1, left M1, left SPL, left AG, right VAA and right V1.

Figure 26: Summary of the between condition MEG Results in Experiment 5 and 6.

4.4 Discussion - Experiment 5

The present study was performed to get a better understanding of the neural network employed during automatic spatial S-R mappings. This was done to compare the neural network during unconscious spatial cueing with the network during automatic imitation to answer the question whether humans have developed a specialized cognitive route to process observed biological stimuli.

Importantly, the behavioural results from Experiments 1 and 2 were replicated, which strengthens the reliability of the SCy effect in the bS-R task and the R-SCy effect in the bOS-R task. As outlined in the Discussion of Experiment 1 and 2, these effects suggest that spatial cues are processed in a neural network that is influenced by top-down processes forming short-term S-R associations based on the task instructions. Although the behavioural effects are consistent with previous studies, the results only provide indirect evidence how spatial cues are processed. Therefore, the MEG analysis was used to pinpoint where in the brain spatial cues are processed in the bS-R and bOS-R tasks to get a better understanding whether spatial cues require a neural network, which is independent of MN areas and thus independent from the cognitive route used by biological stimuli (Sauser & Billard, 2006; Cooper et al., 2013). In the current study, theta, alpha and beta frequencies were compared in the spatially-congruent and spatially-incongruent conditions. This was to done to localize areas, which mediate the facilitation and interference effects of spatial task-irrelevant cues in the bS-R and bOS-R tasks. Hence, the MEG analysis provides direct evidence how spatial cues are processed and, therefore, Experiment 5 is crucial to support the conclusions of Experiment 1 and 2.

4.4.1 Spatial response-conflict and theta band changes

The present study revealed increased theta synchronization in the spatially-incongruent in comparison to the spatially-congruent condition during the bS-R task. This effect was strongest in the S1. Although most research has focused on the role of fronto-medial theta synchronization as an indicator for working memory engagement, parietal theta

synchronization has also been related to such cognitive mechanisms (Klimesch, 1999; Luber et al., 2007; S. Li et al., 2017; Yang, Jacobson, & Burwell, 2017). In the present experiment the greater engagement of working memory was likely required to respond correctly in the more challenging spatially-incongruent condition. This is in line with fMRI research, which shows that responding in an incompatible spatial manner (vs spatial compatible manner) increases the BOLD signal in several parietal areas (Matsumoto, Misaki, & Miyauchi, 2004). This could be linked to the increased theta activity in the present study, since the fMRI BOLD response in frontal and parietal areas is positively correlated to theta synchronization in the same areas (W. Wang, Viswanathan, Lee, & Grafton, 2016). Hence, parietal theta activity is likely important to improve performance in difficult situations such as during the exposure to spatial response-conflict.

Secondly, since the activity was strongest in the S1 the effect could be related to the integration of sensory and movement information (Borich, Brodie, Gray, Ionta, & Boyd, 2016). The S1 integrates sensory information in order to adapt the motor output accordingly. This process should have been more extensive in the spatially-incongruent condition of the bS-R task, since the participants did not rely on learned S-R associations. This could have resulted in increased theta synchronization in the spatially-incongruent in comparison to the spatially-congruent condition. However, this is only a hypothesis and needs to be tested further.

Importantly, the present cluster in the theta band also ranged into the SMA. To date, theta synchronization in this area has been related to spatial conflict during the Simon task (Cohen et al., 2008; Nigbur et al., 2011). It is widely agreed that increased fronto-medial theta synchronization during the spatially-incongruent in comparison to the spatially-congruent condition in the Simon task is related to increased working memory processes, which trigger top-down control mechanisms (Cohen & Ridderinkhof, 2013; Phillips, Vinck, Everling, & Womelsdorf, 2014). Past studies required participants to respond with the right and left hands according to non-biological stimuli on the screen, whereas the current study only used right-handed responses. Although it has long been shown that

an unimanual paradigm elicits Simon effects (Heister, Ehrenstein, & Schroeder-Heister, 1987), this is the first study, which shows that conflict related (frontal) medial theta is elicited by an unimanual Simon like S-R paradigm. Further, the reported studies have used shapes instead of socially relevant biological stimuli as in the present study (Cohen et al., 2008; Nigbur et al., 2011). This shows that frontal theta effects are not affected by stimulus type but that they are elicited whenever spatial response-conflict occurs. No correlation between the behavioural SCy effect and differences in medial theta activity between conditions was observed. Previous studies have also not found any correlation between medial theta synchronization and the behavioral data in a Simon-like S-R task. In contrast, positive correlations between medial theta power and RTs have been revealed, indicating that slower responses are guided by more theta synchronization (Cohen, 2011).

No significant effects in the theta range were found in the bOS-R task. This was surprising, since a study has reported increased theta band synchronization in the spatially-congruent condition in comparison to the spatially-incongruent condition in an OS-R task (Cao et al., 2017). However, they only used a single electrode and no source localization, in contrast to, the whole brain analysis with subsequent source localization in the current study. Hence, differences in methodology could have caused the differences in the results.

It has been suggested that S-R and OS-R tasks rely on different cognitive and neural mechanisms (De Jong et al., 1994). The absence of frontal theta synchronization in the OS-R task could support such interpretations. Further, an LRP analysis has shown that SCy and R-SCy mechanisms interact in succession during an OS-R task (See, Appendix D Section: ***Event-Related Potentials and SCy***). For example, during spatially-congruent trials in the OS-R task the stimulus contralateral hemisphere is activated first. This is interrupted by the activation of the stimulus ipsilateral hemisphere before the stimulus contralateral hemisphere is activated again and the correct response is executed (De Jong et al., 1994). Such mechanisms would create conflicting activity in the MEG data, which could cancel each other out and thereby explain why no significant differences were found between spatially-congruent and spatially-incongruent conditions in the

bOS-R task.

4.4.2 Spatial response-conflict and alpha band changes

In the bS-R task more alpha desynchronization was found in the spatially-incongruent condition in comparison to the spatially-congruent condition in the CN. Alpha desynchronization has been positively correlated with the fMRI BOLD response and is therefore, interpreted as increased activity of the affected area (Laufs et al., 2003). CN activity is associated with the evaluation and execution of rule-bound actions (Grahn, Parkinson, & Owen, 2008). In Simon tasks increased CN activity has also been found during spatial response-conflict (Peterson et al., 2002; Liu et al., 2004; Kerns, 2006), although such effects probably depend on the magnitude of the perceived conflict (Ali, Green, Kherif, Devlin, & Price, 2010). In the current experiment, the usage of unimanual responses activating the same hemisphere could have increased the perceived spatial conflict. Secondly, the usage of biological cues, which are socially relevant, could have increased alertness and triggered the differences in CN activity between spatially-congruent and spatially-incongruent conditions. Hence, the present study confirms that CN activity is important for inhibiting or controlling S-R mappings (Shadmehr & Holcomb, 1999; C.-s. R. Li, Yan, Sinha, & Lee, 2008) and when an automatic response needs to be stopped (Vink et al., 2005). Importantly, none of the presented experiments have found CN activity during spatial response-conflict using MEG or EEG recordings. Therefore, the current study is the first, which reveals alpha desynchronization in the CN during spatial response-conflict while using a Simon-like S-R task.

Interestingly, there was a borderline negative correlation between the difference in CN activity between conditions and the behavioural SCy effect. In other words, the more the CN desynchronized in the spatially-incongruent condition in comparison to spatially-congruent condition, the larger the behavioural SCy effect. This effect can be explained by a study of MacDoland et al. (2011), who illustrated that the posterior striatum, which included the CN, was activated when people withheld a response to answer more deliber-

ately. In the study, Parkinson patients were tested on a decision-making task. Participants reacted to number pairs presented on the screen based on a simultaneously presented cue (frame around the number pair). If the frame was bold participants reacted to the larger number and when the frame was thin participants reacted to the smaller number. The experiment used verbal responses. Congruency was manipulated by presenting two number pairs consecutively. On congruent trials the target number (e.g. three) in the first pair and second number pair was always the smallest (e.g. three vs four and five and three) or the largest number (e.g. three vs one and two and three). On incongruent trials, the target number was the smallest in one number pair and the largest in the other pair (e.g. three vs four and two and three). In the congruent in comparison to incongruent condition responses were faster. When the patients were on Levadopa, which increased CN activity, RTs increased during incongruent and congruent trials. In other words, the posterior striatum was used to control the responses, which led to increased RTs. If this interpretation is correct, the results of the current study show that increased CN activity is associated with slower and more deliberate responses on conflict trials in a Simon-like task. On the other hand, less CN activity on spatially-congruent trials should be associated with faster and more automatic responses (MacDonald et al., 2011). Hence, CN activity is important when participants engage in controlled responding, trying to execute the correct response in the presence of a task-irrelevant spatial cue.

In the bS-R task alpha also desynchronized more on spatially-incongruent in comparison to spatially-congruent trials from 400 to 700 ms in the bilateral LG and left SPL. Many studies using fMRI recordings have reported increased BOLD responses in parietal areas during perceived conflict (Bush, Shin, Holmes, Rosen, & Vogt, 2003; Dassonville et al., 2001; J. Fan, Flombaum, McCandliss, Thomas, & Posner, 2003). Evidence from MEG research using a Simon paradigm shows that posterior alpha desynchronization during spatially-incongruent trials is related to performance adjustments on the proceeding trial and not to active conflict management (Cohen & Ridderinkhof, 2013). This hypothesis is supported by research showing that posterior alpha can be correlated with performance

on the following trial (Compton, Arnstein, Freedman, Dainer-Best, & Liss, 2011; Cohen et al., 2012). The current study, found no correlation between the behavioural SCy effect and the differences in posterior alpha power between conditions. Therefore, it is likely that posterior alpha changes were not related to 'online' conflict management.

Interestingly, posterior alpha power showed a reversed pattern in the bOS-R task: increased posterior desynchronization in the spatially-congruent condition in comparison to the spatially-incongruent condition. Although these results were visible in the sensor level plots, they were not statistically reliable. If posterior alpha is related to the adjustment of behaviour on the following trial, the visible switch between bS-R and bOS-R tasks could be an indicator that spatially-congruent cues in the bOS-R task trigger more behavioural adjustments, whereas the opposite effect is seen in the bS-R task. This effect could dissociate the neural underpinnings of SCy and R-SCy effects.

4.4.3 Spatial response-conflict and beta band changes

The bS-R task did not reveal any significant changes in the beta band depending on SCy. The results were clearly limited to lower frequency bands. This was the case for the bS-R as well as bOS-R tasks. Therefore, it is likely that SCy is not guided by changes in the beta band. Only one study has reported reliable conflict related changes in the beta frequency (Brittain et al., 2012). However, this study used a Stroop and not a Simon-like task. [26]. Further intracranial recordings from the subthalamic nucleus were used, which have a much higher signal sensitivity than MEG recordings. Hence, the differences between the results in this study and the current experiment are probably due to differences in the experimental design or the used technology.

[26]In the Stroop task participants observe colour words, which are displayed in different colours. Participants are asked to name the colouring and disregard the word semantics. On congruent trials the written and coloured information match, whereas it is not matching in the incongruent condition. Hence, the Stroop task evokes stimulus-conflict

4.4.4 Summary: The neural correlates of SCy

All in all, the effects of the present study have shown that SCy is mediated by two mechanisms. First, medial theta increases during conflict to trigger top-down mechanisms and guide responding. Similarly, theta power increases in the S1 during spatially-incongruent trials could facilitate more demanding S-R mappings. Lastly, CN activity increases during conflict to respond more controlled and deliberately. Importantly, none of these areas have been associated with the classical MN system (the IFG, vPMC and IPL; (Molenberghs et al., 2012; Kilner & Lemon, 2013). Therefore, it is likely that spatial cues are not processed in areas that are typically ascribed to the processing of biological stimuli. This is in line with the computational model from Sauer and Billard (2006), which proposes that SCy, in contrast to BCy, is processed outside of the MN system. Accordingly, the PPC is involved in S-R mapping of observed spatial stimuli and the PFC serves a control function, which updates the mapping by integrating contextual information. In the present study, both the PPC and the PFC were not related to the management of spatial conflict. Therefore, an alternate neural circuit is proposed, which includes the the S1, the SMA as well as the CN. However, since only the CN activity showed a correlation with the behavioural SCy effect and studies have shown that CN activity is important for learning S-R associations (Seger, 2005), it is likely that CN activity is crucial to update the S-R mapping according to the task rules.

Unfortunately, the study did not find that any significant effects related to the R-SCy effect in the bOS-R task and hence no neural evidence for the S-R recoding was found. However, visually posterior alpha showed the opposite trend in the bOS-R task than in the bS-R task. Meaning that more posterior alpha synchronization was found in the spatially-congruent condition in the bOS-R task and not in the spatially-incongruent condition as in the bS-R task. It is difficult to make any conclusion based on null findings. Nevertheless, these observed tendencies could represent the neural changes underlying logical recoding of the task-irrelevant stimulus in the bOS-R task. Lastly, it is likely that the bOS-R task was more difficult than the bS-R task, since the average RTs were much longer in the

former compared to the latter. This increase in difficulty could have created a sealing effect in areas such as the CN so that no further activation was required to overcome the spatial response-conflict. This could also explain why no neural effect of spatial congruency was found in the OS-R task.

4.4.5 Conscious imitation and Counter-Imitation

The present study also measured the neural correlates accompanying conscious imitation and counter-imitation. The behavioural results replicated the effects observed in Experiment 2: faster responses during conscious imitation in comparison to counter-imitation. Although the focus of the experiment was to assess automatic imitation, it was of interest whether conscious imitation would elicit MN activity. Theta, alpha and beta frequencies were used to compare rest to action preparation periods. bS-R and bOS-R tasks only differed in the theta band. Whereas the former showed increased synchronization in the TP, PO, MFG and PFC during action preparation in comparison to rest. No frontal differences in the theta band was observed in the bOS-R task. Frontal theta is an indicator of cognitive control (Cavanagh & Frank, 2014), working memory engagement (Itthipuripat et al., 2013) , behavioural adaption (Cavanagh et al., 2012), and it has been related to better task performance (Cohen & Cavanagh, 2011). Hence, it was expected to observe more frontal theta synchronization during action preparation in comparison to rest. That no difference in frontal theta between action preparation and rest was found in the bOS-R task was not expected, since frontal theta increases with task difficulty (Jensen & Tesche, 2002).

For alpha and beta frequencies the neural pattern in the bS-R and bOS-R tasks were strikingly similar. Both frequency bands showed broad posterior desynchronization during action preparation in comparison to rest. In general, posterior alpha and beta desynchronization have long been associated with increases in attention. Hence, the observed effects are likely related to the increased attention during response preparation in comparison to rest (Gola et al., 2013; Siegel et al., 2008). In addition, beta desynchronization was also

found over the left M1, which was expected due to the preparation and execution of a voluntary motor response (Kilavik et al., 2013).

These results highlight one problem in the current imitation literature. Many studies have reported mu, alpha or beta desynchronization in central or posterior regions during imitation and have interpreted this to MN activity (Fox et al., 2016). However, since many of these studies focused on the analysis of EEG channels above the M1 and S1, it is likely that they have confused posterior alpha and beta processes related to attention with MN activity (Hobson & Bishop, 2017). In the present study, it is clearly shown that sensorimotor beta and alpha activity is not related to mirroring during imitation, since a very similar neural pattern was observed during counter-imitation, during which MN activity needs to be inhibited.

5 Chapter 5

5.1 Introduction - Experiment 6

The present study was set up to measure the neural correlates of automatic imitation. In Experiment 3 and 4 BCy effects were found in the sS-R tasks and R-BCy effects were found in the sOS-R tasks. Hence, the behavioural effects for biological and spatial cues were very similar. The presence of R-SCy and R-BCy effects shows that the neural processes involved in the S-R mappings are influenced by task instructions (Proctor et al., 2011). In the OS-R tasks only fast responses should have been in accordance with the learned S-R associations, since slower and more deliberate processes should have adapted these associations in favor of the short-term S-R rules determined by the task instructions (R. K. Ridderinkhof, 2002). However, Experiment 1 to 4 clearly showed that logical recoding of the S-R mappings took place before participants responded, which means that long-term S-R associations were controlled immediately. Hence, R-SCy and R-BCy effects were similarly influenced by short-term S-R associations, which stresses that biological and spatial stimuli probably use similar neural networks as well.

As mentioned in the General Introduction, most studies investigating automatic imitation have used behavioural paradigms. Although behavioural studies provide potential insights into the neural mechanisms during automatic biological and spatial cueing, brain imaging studies are required to validate these results. Automatic imitation – the process during which task-irrelevant biologically-congruent stimuli facilitate behaviour whereas biologically-incongruent stimuli interfere with behaviour – has not been assessed using MEG and EEG recordings (Heyes, 2011). However, fMRI and TMS studies provide valuable insights about the neural networks during automatic imitation.

5.1.1 Measuring the neural correlates of automatic imitation

The research on automatic imitation using TMS and fMRI have focused on two slightly different paradigms, which already have been outlined in the General Introduction. First,

S-R paradigms as used in the present study has been applied. Here task-irrelevant biological or spatial stimuli manipulate whether responses are congruent or incongruent whilst participants respond to a imperative stimulus (Brass et al., 2005; Catmur et al., 2009; Mengotti et al., 2012). Secondly, simple response paradigms have been used. Here no task-irrelevant cue is presented and stimulus compatibility is only manipulated by the task-relevant stimulus. Participants respond to the task-relevant biological or spatial cue with a predefined action throughout an experimental block (Brass et al., 2001; Cross et al., 2013; Newman-Norlund, Van Schie, Van Zuijlen, & Bekkering, 2007). S-R and simple response paradigms show that congruent/compatible cues facilitate behaviour, whereas incongruent/incompatible cues interfere with behaviour [27].

5.1.2 Limitations in the experimental designs

Brass (2001) pioneered in assessing the neural correlates of automatic imitation using a simple response paradigm. He found that compatible in comparison to incompatible biological stimuli or movement trajectories elicited increased activity in the dorsolateral PFC, FPC, anterior parietal cortex and precuneus. However, since these results were not compared with the neural correlates during spatial S-R mapping, it is difficult to know whether the observed neural pattern is unique to biological stimuli. In a slightly later experiment, Brass et al. (2005) compared automatic imitation elicited during an S-R paradigm to the neural processes during a Stroop task. Biological cues in the S-R paradigm in comparison to the non-biological stimuli in the Stroop task showed increased activity in the fronto-medial cortex, IFG, precuneus, AG and TPJ. Although the neural processes during automatic imitation were compared to the neural mechanisms during a non-biological cueing paradigm, the results were still problematic, since two different paradigms, which by themselves elicit different cognitive processes, were used. Whereas the S-R task triggers response-conflict the Stroop task evokes stimulus-conflict (See, Introduction - Experiment 1 and 2) (Scerrati, Lugli, Nicoletti, & Umiltà, 2017). Therefore,

[27] Congruency is used when the effect is evoked by a task-irrelevant stimulus and compatibility is used when the effect is elicited by a task-relevant cue.

it is not possible to determine whether the observed neural differences between tasks were due to the nature of the cues or the nature of the elicited conflicts.

5.1.3 Comparing the neural correlates of BCy and SCy effects

Newer studies have focused on including control conditions in which the only difference between biological and non-biological effects is the nature of the cue. Cross et al. (2013) replicated the study of Brass et al. (2001) but included biological and spatial simple response tasks. Since the experiments only differed in cue type this study could pinpoint the neural effects associated with the cue type more precisely. The biological compatibility effect (increased RTs in the incompatible in comparison to compatible condition) revealed unique significant activity in frontal areas (IFG, medial PFC, ACC), the anterior insula, SPL, CN and the cerebellum when the neural activity in the compatible condition was subtracted from the neural activity in the incompatible condition. In contrast, spatial compatibility effects did not reveal any unique activity above the neural pattern observed when eliciting biological compatibility effects. Further, biological in comparison to spatial cues increased the neural connectivity between the medial PFC and the ACC. In conclusion, simple response studies show that frontal and parietal areas are crucial for biological compatibility effects.

Bien et al. (2009) also replicated the study from Brass et al. (2005) to ensure that the neural BCy effect was compared to the spatial equivalent. Instead of comparing automatic imitation to the Stroop interference effect, bS-R and sS-R tasks were used. A spatial stimulus (a cross making a vertical movement) was superimposed on a biological stimulus (a hand making a finger tap with the index or middle finger). Participants used the right hand and tapped with the index or middle finger. In the sS-R task, participants tapped with the finger, which corresponded to the hemifield where the cross was presented. Simultaneously, the task-irrelevant biological stimulus performed a tapping movement, which could either be biologically-congruent or biologically-incongruent with the response triggered by the cross. In the bS-R task, the participants were instructed to respond

with the same finger as the one tapping on the screen while the task-irrelevant cross was spatially-congruent or spatially-incongruent with the response. While participants performed the tasks fMRI or TMS were used. The results revealed that the left PO, also named frontal operculum, was uniquely activated during biologically-incongruent trials when automatic imitation needed to be inhibited. When targeting different areas with TMS, stimulation to the right PMC improved RTs on biologically-incongruent trials, which led to the conclusion that the right PMC is supporting mirroring. Interestingly, the PMC has long been related to MN activity and, hence, the study showed that MNs are important for automatic imitation (Rizzolatti & Craighero, 2004). Since SCy effects were not associated with activity in the PMC, these results support the direct-matching model from Sauser and Billard (2006), which proposes that direct S-R matching during automatic biological cueing is guided by vPMC activity whereas spatial S-R mapping is taking place outside MN areas. Further, Bien et al. (2009) found that the MFG is important for generic response inhibition unrelated to the stimulus type. This is supported by an MEG study showing that the MFG is activated by working memory engagement and not specifically during spatial or biological S-R mapping (Roux & Uhlhaas, 2014).

Although the last two studies did attempt to create a valid baseline, which could be compared with automatic imitation, they still suffered from similar limitations as the first behavioural studies comparing spatial and biological S-R contingencies. Among others, this means that the biological stimulus incorporated spatial characteristics and, hence, it was not possible to directly link the neural activity to its biological features (See, Introduction - Experiment 3 and 4).

Recent work has addressed this limitation in brain-imaging studies. For example, Mengotti et al. (2012) used the paradigm of Boyer et al. (2012) while employing fMRI recordings. Participants performed automatic imitation as well as automatic spatial cueing tasks similar to Experiment 1 and 3. The fMRI analysis revealed that automatic and conscious imitation activated the parietal operculum (PaO) corresponding to the frontal part of the IPL. Unfortunately, the difference in BOLD response between biologically-

incongruent and biologically-congruent trials was not assessed in the sS-R and bS-R tasks separately. Instead the BOLD response between conditions in the bS-R task (spatially-congruent minus spatially-incongruent) was subtracted from the BOLD response between conditions in the sS-R task (biologically-congruent minus biologically-incongruent) [28]. This revealed increased activity in a wide cognitive network including MN areas such as the right IPL and the right IFG but also many areas unrelated to MN activity such as the bilateral amygdala and the bilateral SMA. This could either suggest that the mentioned areas were crucial for spatial S-R mapping during spatially-congruent trials. Secondly, the mentioned areas could be activated by biologically-incongruent trials and thus be important for inhibiting automatic imitation.

A follow up TMS experiment stimulated the PaO (IPL) while participants performed the same tasks (Mengotti et al., 2013). TMS abolished the BCy effect but had no effect on the SCy effect. These results led to the conclusion that PaO activity uniquely supports automatic imitation. Hence, the studies confirmed prior experiments suggesting that spatial and biological stimuli are processed in different cognitive routes (Sauser & Billard, 2006).

Lastly, Catmur et al. (2009) used TMS to the left IFG while participants engaged in automatic imitation or automatic spatial cueing. Stimulation of the left IFG eliminated the automatic imitation effect (incongruent - congruent condition) whereas it had no influence on spatial congruency. Whether no automatic imitation effect was observed because RTs in the biologically-congruent condition increased or RTs in the biologically-incongruent condition decreased was not clarified. However, evidence from other studies would suggest the latter. First, an increased BOLD response in frontal areas including the left IFG is observed during biologically-incongruent in comparison to biologically-congruent trials (Cross et al., 2013). Secondly, the left PO could be the gate-keeper for imitation, controlling mirroring whenever this is detrimental for performance (Bien et al., 2009). Hence, activity in the left IFG is likely crucial when stopping automatic

[28]Note that the subtraction between congruent and incongruent conditions was reversed in comparison to the subtraction performed in the present study.

imitation. These findings go against the MN hypothesis, which suggests that the IFG triggers imitation, since it maps observed movements directly onto the observer's motor system (Iacoboni, 2005). Catmur et al. (2009) also stimulated the PPC but it had no effect on B-Cy or S-Cy effects. These results disprove the suggestion of Sauser and Billard (2006) that spatial S-R mappings is guided by the PPC. In Experiment 5, the left CN was associated with controlled (slower) responding on spatially-incongruent trials in comparison to spatially-congruent trials. Therefore, it was suggested that CN activity guided rule-bound spatial S-R mappings during the bS-R task. Based on the studies above the left IFG could have a similar role during biological S-R mappings.

In sum, the experiments assessing the neural correlates of automatic imitation and automatic spatial cueing have concluded that biological and spatial stimuli are processed in different neural routes in accordance with the direct-matching model (Sauser & Billard, 2006). This contradicts the behavioural results found in Experiment 1 to 4, which showed very similar results for both stimulus types. Hence, it was suggested that biological and spatial stimuli use similar cognitive processes (e.g. learned long-term S-R associations, which are controlled by short-term S-R rules) to elicit the respective congruency and reversed congruency effects. The present study is necessary to conclude whether similar behavioural effects triggered by spatial and biological task-irrelevant stimuli can be evoked by two different neural networks.

5.1.4 Using MEG to measure automatic imitation

To date the focus has been on fMRI and TMS when assessing the neural correlates of automatic imitation using S-R or simple response paradigms. With the excellent temporal resolution of MEG fast paced cognitive processes during automatic imitation can be discerned better. For example, MEG studies assessing SCy effects have used time windows as short as 300 or 400 ms while assessing alpha and theta bands (Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). In contrast, fMRI research examining SCy and BCy effects average the BOLD response over several seconds (Liu et al., 2004; Kerns, 2006).

Therefore, the present MEG study enables a more differentiated investigating into the neural underpinnings of automatic imitation.

Secondly, by assessing the neural dynamics of automatic imitation and automatic spatial cueing in the theta, alpha and beta frequencies one could potentially reveal that automatic imitation and automatic spatial cueing affect different frequency bands, which would dissociate the processing of spatial and biological cues as well. (Cohen et al., 2008; Nigbur et al., 2011; Cohen & Ridderinkhof, 2013; Fox et al., 2016; Hobson & Bishop, 2017).

Lastly, this is the first study investigating the neural characteristics of the R-BCy effect, which shows that biological S-R mappings are influenced by top-down processes (De Jong et al., 1994; Sauser & Billard, 2006). By assessing the neural mechanisms leading up to the R-BCy effect, it is possible to examine which brain areas adjust the biological S-R mapping to fit the task rules. Interestingly, findings exist, which show that the left IFG becomes increasingly activated when an observed action is not performed in the correct context. Earlier it was mentioned that the left IFG likely controls imitation (Bien et al., 2009). However, these results suggest that the left IFG also updates biological S-R mappings based on short-term S-R associations.

5.1.5 Hypotheses and experiment preview

Based on the results from fMRI and TMS studies illustrated above, it was hypothesized that the left IFG is important for controlling automatic imitation by taking the task instructions into account. More activity in the IFG should be observed during biologically-incongruent in comparison to biologically-congruent trials in the sS-R task. This could be visualized by increased alpha or beta desynchronization during biologically-incongruent trials. Secondly, a reversal of this pattern in the sOS-R task would indicate that logical recoding had occured on a neural level and that the left IFG processes biological stimuli depending on the context. This would provide evidence that biological stimuli are not processed in a direct S-R matching network. Further, it was expected to observe fronto-medial theta synchronization due to biological response-conflict (Cohen et

al., 2008). However, since biological stimuli trigger less fronto-medial theta synchronization in comparison to spatial cues, the effect should be attenuated in comparison to the effect observed in Experiment 5. (Urgen et al., 2013).

5.1.6 Conscious spatial cueing and counter-cueing

The present study also examined conscious spatial cueing and counter-cueing to compare the neural signatures with the results from conscious imitation and counter-imitation. As mentioned in the Introduction to Experiment 5 conscious imitation evokes a wider neural network than conscious spatial cueing. For example, Mengotti et al. (2012) reported that conscious spatial cueing did not show any unique neural activation over and above the neural network associated with conscious imitation. On the other hand, conscious imitation revealed a wide variety of areas showing significant more activation than during conscious spatial cueing (e.g. occipital cortex, IPL and SPL, central gyri as well as subcortical regions such as the left insula and bilateral amygdala). These results were supported by two studies: first, Désy and Lepage (2013) reported greater parietal cortex activation during the imitation of biological movements in comparison to the 'imitation' of non-biological stimuli. Secondly, Kessler et al. (2006) found increased desynchronization in the alpha range over the whole cortex during conscious imitation in comparison to conscious spatial cueing, which indicates that the former increases cortical activation more than the latter. In all, these findings show that conscious spatial cueing does not evoke extensive neural activation in comparison to conscious imitation. Therefore, the changes in theta, alpha and beta frequencies would likely be related to generic responding mechanisms and not to the spatial cue per se. However, when assessing conscious imitation in Experiment 5 it was not possible to attribute any neural activation during action preparation in comparison to rest to the biological nature of the imperative stimulus. Hence, it is hypothesized to see very similar neural patterns when contrasting action preparation and rest periods during conscious spatial cueing. That is, in the sS-R and sOS-R tasks frontal theta should show increased synchronization during action prepara-

tion in comparison to rest, which would indicate increased working memory engagement during the former (Cohen et al., 2008; Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). Alpha and beta activity in parietal and visual areas should desynchronize during action preparation in comparison to rest as an indicator of increased visual attention (VanRullen & Thorpe, 2001). Lastly, beta activity should desynchronize over the left motor cortex due to the preparation and execution of voluntary actions during the action preparation period in comparison to rest (Kilavik et al., 2013). The present experiment repeated the mixed sS-R and sOS-R tasks of Experiment 4 while recording MEG data to assess the neural correlates of automatic imitation and conscious spatial cueing.

5.2 Methods - Experiment 6

5.2.1 Participants

The materials, procedure, data processing and analysis were very similar to Experiment 5. The few differences between the present experiment and the prior MEG experiment are described next.

5.2.2 Participants

24 participants took part in the experiment. All experimental procedures complied with the Declaration of Helsinki and were approved by the Aston University, Department of Life and Health Sciences ethics committee. Participants gave written informed consent before taking part in the study. Three participants were excluded from the analysis since they made too many errors or responded to slow, which decreased the sample to 21 participants (9 males, Mean age = 27 SD = 2.2).

5.2.3 Material, procedure and acquisition

In the present experiment participants performed the sS-R and sOS-R tasks described in Chapter 2. Else the materials were similar to Experiment 5 (Figure 20). Since RTs were shorter in the spatial tasks than in the biological tasks a shorter inter-trial interval was required in the present experiment than in the previous MEG experiment. The first 3 participants had an inter-trial interval of 1500 ms, which was increased for the remaining participants to 1872 ms. This was done to ensure that the beta rebounds did not influence oscillations on the proceeding trial. The experiment had 400 trials in total with 100 trials for each condition. More trials could be included than in the previous MEG experiment, since the inter-trial interval was 528 ms shorter in the present experiment.

5.2.4 Sensor analysis

For the sensor analysis the theta, alpha and beta frequencies were examined. The TFR plots showed that the alpha band were positioned slightly higher (9-13 Hz) than in the

bS-R and bOS-R tasks in the previous MEG experiment. The alpha band varies slightly between individuals, which could have caused the differences in alpha signature between the current (9-13 Hz) and the previous MEG experiments (8-12 Hz; Bazanova and Vernon, 2012).

5.2.5 Source analysis

The present source analysis used a different taper than in the prior MEG experiment. Whereas a hanning taper was used for the bS-R and bOS-R tasks, the current experiment used a Slepian sequence taper (dpss) when localizing alpha and beta frequencies. The difference in taper between datasets was due to the different frequency signatures. Whereas the current spatial task (measuring implicit biological congruency) showed a broadband (Figure 29) signature the biological task (measuring implicit spatial congruency) described in the previous chapter showed more concise changes in lower frequency bands (Figure 24). The dpss taper is better in picking up broadband signatures because of two reasons: first, the taper allows for more spectral leakage and secondly, it is possible to specify frequency smoothing using a dpss taper but not using a hanning taper. Therefore, a dpss taper was used for the current task in the alpha and beta bands, but not for the theta band, which was more specific in frequency and was therefore localized using a hanning taper. The calculations for the virtual electrode and the correlations between MEG data and behavioral data were the same as in the prior MEG experiment.

5.2.6 Choosing the time period of interest

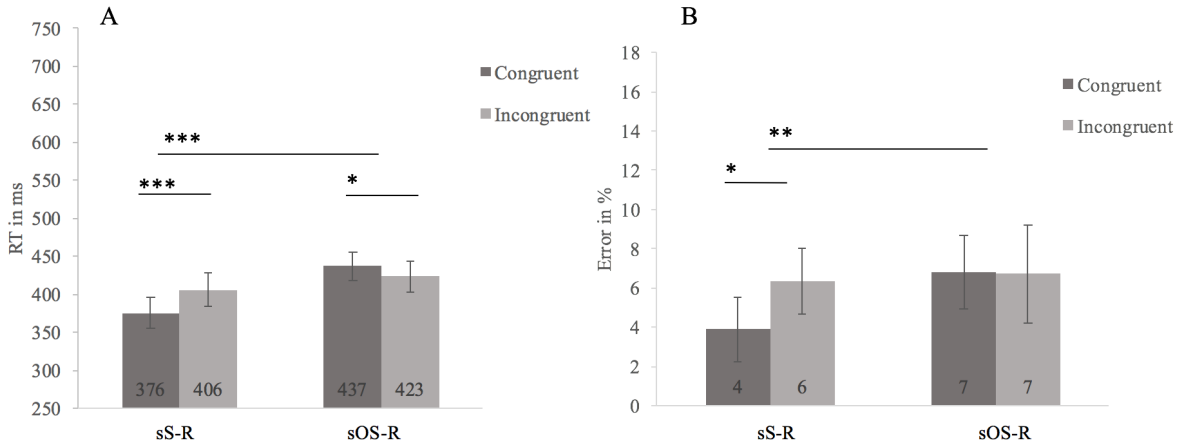
The time period of interest was chosen according to the length of the RTs, as in the bS-R and bOS-R tasks (Experiment 5). However, since the RTs in the present experiment were shorter the upper cut-off in the sS-R and sOS-R tasks was 600 ms. Hence, a period from 0 to 600 ms after stimulus movement onset provided the guideline to examine action preparation.

5.3 Results - Experiment 6

5.3.1 Behavioural results

RTs in sS-R and sOS-R tasks are shown in Figure 27A. The repeated measures ANOVA with TASK (sS-R / sOS-R) and biological CONGRUENCY (biologically-congruent / biologically-incongruent) as factors revealed a significant main effect of TASK, $F(1,19) = 42.42$, $p<0.001$, $\eta^2=0.74$. Participants reacted faster in the sS-R task in comparison to sOS-R task (390 ± 96 ms vs 430 ± 87 ms, $p<0.001$). A significant main effect of biological CONGRUENCY, $F(1,19)=4.84$, $p<0.05$, $\eta^2=0.23$ indicated that responses on biologically-congruent trials were faster than responses on biologically-incongruent trials (406 ± 92 ms vs 414 ± 95 ms, $p<0.05$). A significant TASK x biological CONGRUENCY interaction, $F(1,19)=39.12$, $p<0.001$, $\eta^2=0.72$, revealed that participants responded 30 ms faster on biologically-congruent trials in comparison to biologically-incongruent trials in the sS-R task (375 ± 94 ms ± vs 405 ± 98 ms, $p<0.000$) but 13 ms faster on biologically-incongruent trials in comparison to biologically-congruent trials in the sOS-R task (436 ± 82 ms vs 423 ± 93 ms, $p<0.05$).

Error rates from the sS-R and sOS-R tasks are shown in Figure 27B. The repeated measures ANOVA with TASK (sS-R / sOS-R) and biological CONGRUENCY (biologically-congruent / biologically-incongruent) as factors revealed a significant main effect of TASK, $F(1,19)=2.93$, $p<0.01$, $\eta^2=0.14$. Participants made less errors in the sS-R task in comparison to the sOS-R task (5.1 ± 6.1 % vs 6.7 ± 9.7 %). No effect of biological CONGRUENCY, $F(1,19)=1.54$, $p>0.05$, $\eta^2=0.08$. but a significant TASK x biological CONGRUENCY interaction, $F(1,19)=8.96$, $p<0.01$, $\eta^2=0.30$, which stems from less errors on biologically-congruent trials in comparison to biologically-incongruent trials in the sS-R task (3.8 ± 4.3 % vs 6.3 ± 7.4 %, $p<0.05$) but no difference between biologically-congruent and biologically-incongruent conditions in the sOS-R task (6.8 ± 8.4 % vs 6.7 ± 11.1 %, $p>0.05$).



*** P<.001 ** P<.01 * P<.05

Figure 27: shows the reaction times and error rates in the sS-R and sOS-R tasks. (A) Participants reacted faster in the sS-R than in the sOS-R task. In the sS-R task RTs were faster in the biologically-congruent in comparison to biologically-incongruent condition. This was reversed in the sOS-R task. (B) More errors were made in the sOS-R task in comparison to the sS-R task. In the sS-R task more errors were made in the biologically-incongruent condition in comparison to the biologically-congruent condition.

5.3.2 MEG results

To answer the question whether task irrelevant biological stimuli are processed in accordance with the direct-matching model (Sauser & Billard, 2006) in mirror neuron areas, brain activity in the theta, alpha and beta bands were compared during biologically congruent and biologically incongruent trials. It will further be of interest to assess whether activity in mirror neurons areas differ when task irrelevant biological stimuli are beneficial for responding and when they need to be inhibited. This would provide insights how mirror neuron areas foster automatic imitation. Here only the significant results are shown, which help to answer these questions of interest. However, for a summary of all results in the between condition analysis of the sS-R and sOS-R tasks see Figure 22.

The effects of biological congruency in the theta band: Figure 28A shows the topoplots of the differences between biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) in the theta band during action preparation. The biologically-incongruent condition revealed less theta power than the biologically-congruent condition between 0 to 300 ms in left fronto-central channels and in left parietal

channels between 300 to 600 ms. The difference TFR (incongruent – congruent condition) of the left fronto-central channels shows negative activity between 0 and 500 ms in the theta range (4-7 Hz), which is due to increased theta synchronization in the biologically-congruent in comparison to biologically-incongruent condition Figure 28B. A sensor level permutation test between 0 to 600 ms revealed a significant negative cluster between 0 to 300 ms in left frontal and central channels in accordance with the topoplots Figure 28A. To localize this activity a DICS beamformer with the time window from 0 to 500 ms was performed. It did not reveal any significant sources but the strongest source was over the left S1 cortex (MNI -30 -35 48) and the left M1 (MNI -30 -24 68; p=0.09; Figure 28C). A virtual electrode was placed into the left S1 so that the average power of the theta band (4-7 Hz), time-locked to the movement onset of the imperative stimulus, could be calculated for each condition Figure 28D. Both conditions showed a synchronization of theta activity after stimulus movement onset, which peaked around 400 ms. From -200 to 700 ms the biologically-congruent condition showed slightly more synchronization than the biologically-incongruent condition. In sum, although the source level effects did not reach statistical significance they are interesting, since the source level cluster is very close to the source level cluster seen in the bS-R task. However, the questions remains whether the observed activity in the current experiment is related to the theta activity seen in medial frontal areas, since it is localized more posterior (Nigbur et al., 2011; Cohen et al., 2008).

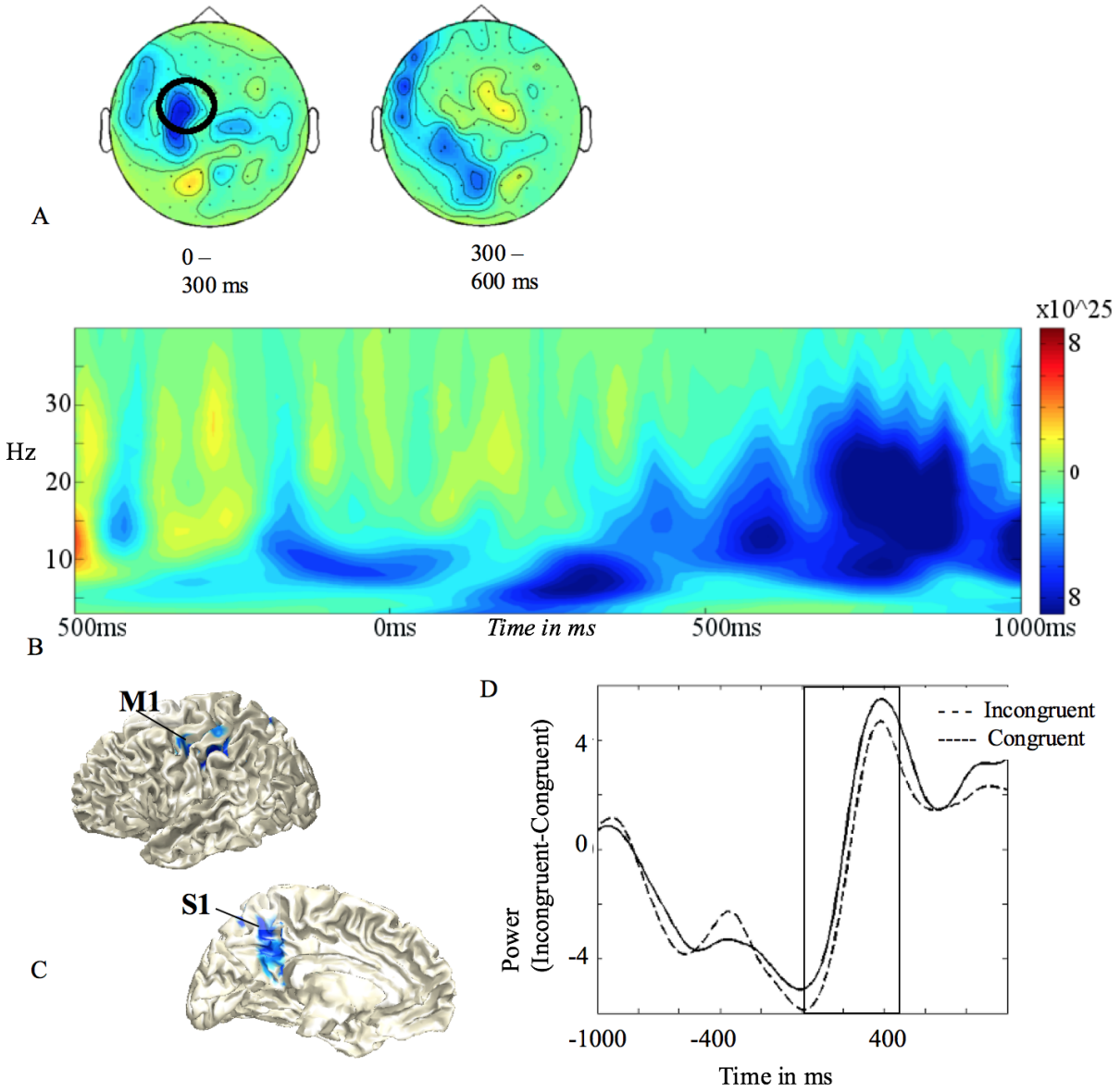


Figure 28: Compares theta band activity in the biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) in the sS-R task. (A) The topoplots of the differences between conditions in the theta band from 0 to 300 ms and from 300 to 600 ms. The black circle indicates the approximate location of the channels used in B (B) A TFR from left fronto-central channels with a relative baseline between -1000 to -700 ms. (C) The output of the source localization from 0 to 500 ms between biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) in the theta band (4-7 Hz) shows a negative cluster in the left S1 and left M1 (D) The output of the virtual electrode placed in the global minimum (S1) of the source level cluster. The power of the theta (4-7Hz) band was averaged for each condition and depicted over time after normalization, using a relative baseline from -1000 to -700 ms. The rectangle corresponds to the time of the beamformer.

The effects of biological congruency in the alpha band: Figure 29A shows the difference topoplots (incongruent - congruent condition) created for the alpha band (8-13 Hz) in the sS-R task. They show negative clusters in parietal and occipital channels throughout the depicted time period (0 to 600 ms). The corresponding difference TFR of the affected posterior channels shows negative activity in the alpha band starting during the onset of the static hand and continuing until approximately 900 ms after movement cue onset with a small gap around 100 ms after movement cue onset. The affected alpha frequency range is centred around 11 Hz (9-13 Hz; Figure 29B). The negative activity in the difference plots is caused by stronger desynchronization in the biologically-incongruent condition as compared to the biologically-congruent condition. Sensor level statistics conducted with the frequency band 9-13 Hz and the time window 0 to 600 ms revealed a significant negative clusters between 300 to 600 ms ($p<0.05$) located in left parietal and occipital channels corresponding to the negative activity seen in the topoplots (Figure 29A). The DICS beamformer analysis of the difference between biologically-incongruent and biologically-congruent conditions (incongruent-congruent condition) from 280 to 600 ms did not reveal significant results. Since the difference TFR of the affected posterior sensors indicated that the identified alpha activity started around 280 ms and lasted until approximately 800 ms, a beamformer with the time window 280 ms to 800 ms was implemented. Importantly, the period from 600 to 800 ms is after the specified period of interest and most likely includes post-response mechanisms. The beamformer revealed a significant cluster ($p<0.01$) with a global minimum in the right V1 (MNI 6 -84 0) and local minima in the left LG (MNI -12 -48 0) and left AG (MNI -30 -60 30; Figure 29C). A virtual electrode in the global minimum did not reveal a good fit with the sensor and source level data. This was probably because it was located at the very edge of a small part of the cluster. Therefore, the virtual electrode was placed at the local minimum in the left LG, which was in the centre of the significant cluster. The virtual electrode is depicted by means of the averaged frequency from 9 to 13 Hz for each condition. It shows alpha band desynchronization in both conditions after stimulus movement onset

(Figure 29D). From approximately 300 ms the conditions diverge and the alpha band activity in the biologically-incongruent condition desynchronizes more than that of the biologically-congruent condition. For the correlation with the behavioural BCy effect statistical testing was applied to the virtual electrode data to select the precise time period during which the biologically-congruent and biologically-incongruent conditions significantly differed. This revealed a significant difference between 400 to 630 ms, (See Appendix E Figure 44). Since the difference between conditions appear relatively early but only reaches significance after 400 ms it is likely that the mechanisms, which causes these differences are present before 400 ms but only reach a certain magnitude after 400 ms. Hence, the observed differences could be related to response preparation. This is especially likely, since the LG and AG have long been related to visuospatial processing during execution and preparation of movements (Cavanna and Trimble, 2006). Further, a positive correlation (two-tailed Spearman correlation $p<0.05$, $r=0.5$, Figure 30A) between the neural (left LG) and behavioral data was found: the larger the differences in desynchronization between biologically-incongruent and biologically-congruent conditions the smaller the (behavioural) BCy effect.

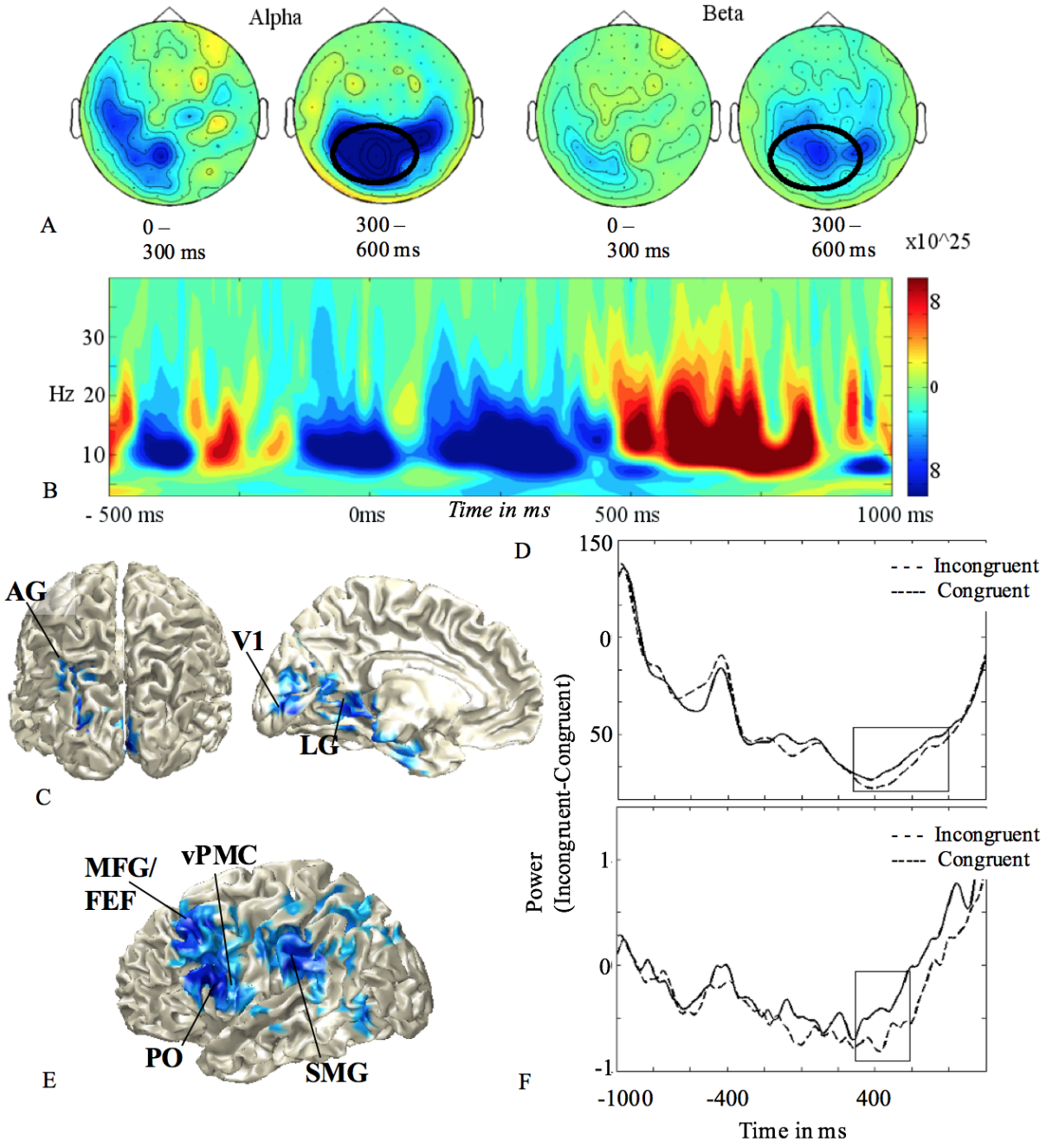


Figure 29: Compares biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) in the alpha and beta bands in the sS-R task. (A) Topoplots of the differences between conditions in the alpha and beta bands from 0 to 300 ms and from 300 to 600 ms. The black circles visualize the channels used in the TFR depicted in B. (B) The difference TFR from posterior channels with a relative baseline between -1000 to -700 ms. (C) The output of the source localization in the alpha band (9-13 Hz) from 280 to 800 ms, which shows a negative cluster in the right V1, left LG and left AG. (D) A virtual electrode located in the local minimum (left LG) of the cluster in C. (E) The output of the source localization in the beta band (13-25 Hz) from 280 to 600 ms, which shows a negative cluster in the left MFG, left FEF, PO, vPMC and SMG. (F) A virtual electrode located in the local minimum (FEF) of the cluster in E. Both virtual electrodes depict the averaged frequency band (alpha or beta) over time with a relative baseline from -1000 to -700 ms. The rectangles correspond to the time of the beamformers.

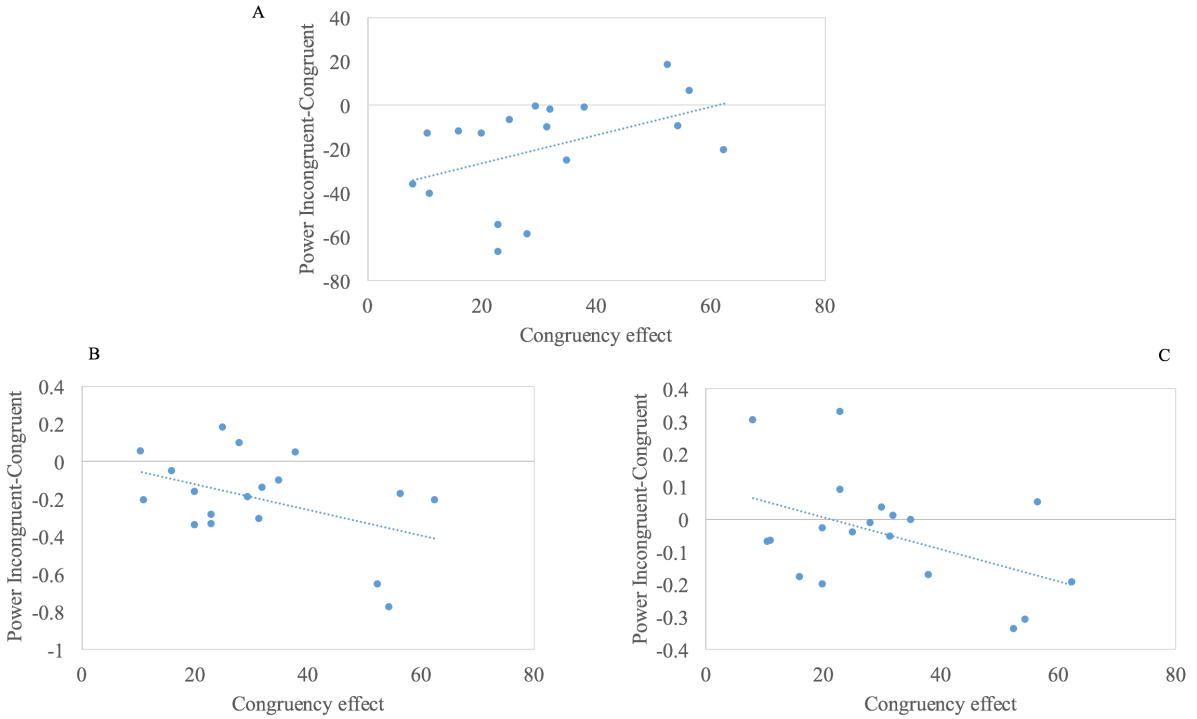


Figure 30: (A) Shows the correlation between the behavioral BCy effects in the sS-R task and the differences in desynchronization between the biologically-incongruent and biologically-congruent conditions of the alpha band in the left LG between 400 - 630 ms. This revealed a significant positive correlation, which showed that a larger difference in desynchronization between conditions was associated with a smaller behavioral BCy effect. (B) Shows the correlation between the behavioral BCy effect in the sS-R task and the differences in desynchronization between the biologically-incongruent and biologically-congruent conditions of the beta band in the left FEF between 410-450 ms and 520-600 ms and in the (C) left PO between 320-360 ms and 390-480 ms. These correlations indicated that a larger difference in beta band desynchronization between conditions was associated with a larger behavioral BCy effect.

The effects of biological congruency in the beta band: Figure 29A shows the topoplots of the differences between biologically-congruent and biologically-incongruent conditions (incongruent - congruent)in the beta band (13-25 Hz) in the sS-R task. It is apparent that the differences in the beta band are similar but slightly attenuated to the topographies seen for the alpha band. The difference TFR (incongruent-congruent condition) of the selection of posterior channels shows beta band desynchronization between 280 to 500 ms after movement stimulus onset, strongest in the lower beta range ($<$ 25 Hz; Figure 29B). Sensor level statistics (13-25 Hz , time window 0-600 ms) revealed a significant clusters in between 220 to 600 ms ($p < 0.05$) starting in left posterior channels and becoming more central after 400 ms. This effect was in accordance with the pattern observed in the topoplots (Figure 29A). To localize the activity in the beta band (13-25 Hz) a DICS beamformer analysis comparing biologically-congruent and biologically-incongruent conditions (incongruent-congruent conditions) from 220 to 600 ms was set-up. Although it revealed a significant cluster in the superior parietal lobule ($p<0.05$), it did not show any frontal activity seen on the sensor level. In contrast, a beamformer from 280 to 600 ms revealed a significant negative cluster ($p<0.01$) in frontal and parietal areas including the left MFG (MNI -32 14 44) and clear local minima in the left frontal eye fields (FEF; MNI -36 24 42) and in mirror neuron areas located in the left IFG such as the PO (MNI -60 12 12) and the vPMC (MNI -48 0 18) as well as the left supramarginal gyrus (SMG) located in the IPL (MNI -54 -30 30; Figure 29E). A virtual electrode in the global minimum (left MFG) at the edge of the cluster did not show a good fit with the data, since it did not reveal a clear difference between biologically-congruent and biologically-incongruent conditions. A virtual electrode positioned in the left FEF, which is part of the MFG, but is located more in the centre of the significant cluster, was more consistent with the source analysis results as the average beta band activity in the biologically-incongruent condition desynchronized more than the average beta band activity in the biologically-congruent condition in the period of interest (280 to 600 ms; Figure 29F). For the correlation with the behavioural BCy effect statistical testing was applied to the virtual electrode data

to select the precise time period during which the two conditions significantly differed. This revealed significant difference between 410 to 450 ms as well as between 520 to 600 ms ($p<0.05$) (Appendix E Figure 44). Additionally, the difference between conditions in the FEF, revealed a borderline negative correlation with the behavioral BCy effect: the stronger the beta band desynchronized in the biologically-incongruent condition in comparison to the biologically-congruent condition, the larger the behavioural BCy effect (Two tailed Pearson correlation $p < 0.07$, r=-0.44; Figure 30B). An additional virtual electrode was placed into the left PO to assess whether activity in an important mirror neuron area would be correlated with the behavioural BCy effect as well. The averaged beta band showed increased desynchronization of the biologically-incongruent in comparison to biologically-congruent condition from 320 to 500 ms. This difference between conditions became significant between 320 to 360 ms and 390 to 480 ms (Appendix E Figure 44). Lastly, a significant negative correlation of the difference in desynchronization between conditions (incongruent-congruent condition) and the behavioural BCy effect was found (two tailed Pearson correlation $p<0.05$, r=-0.46; Figure 30C). The correlation in the PO showed same pattern as the correlation between the neural activity in the FEF and the behavioural data. These results add to the evidence that mirror neuron areas could be involved in the processing of BCy. Taken that beta desynchronization during movement preparation is an indicator of motor readiness, it is interesting to observe enhanced desynchronization in mirror neuron areas when mirroring needs to be omitted. A topic that will be discussed further in the following discussion.

The above results examined the neural effects related to the significant behavioural BCy effect in the sS-R task. The sOS-R task did not reveal any significant results, which could be attributed to the congruency/incongruency of the task irrelevant stimulus during action preparation. In general alpha and beta bands in central and posterior areas were more desynchronized in the biologically congruent condition than in the biologically incongruent condition. Hence these frequencies showed a similar pattern as in the bOS-R task in the previous chapter. The results are shown in the Appendix E.

As in the previous chapter a within condition analysis between rest and action preparation was performed to assess whether conscious spatial cueing would evoke activity outside of mirror neuron areas. However, the results revealed very broad clusters over most of the medial and posterior cortices (Appendix E). Therefore, they were not specific enough to be discerned from the activity pattern observed during conscious biological cueing in the previous chapter. For a summary of all results in the within condition analysis see Figure 26

5.4 Discussion - Experiment 6

The present study was set-up to get a better understanding of the neural network employed during automatic imitation. Especially, it was of interest to assess how the brain is inhibiting the automatic tendency to imitate when imitation is not beneficial. Research using TMS or fMRI has found evidence that left fronto-lateral and parietal areas are important when automatic imitation is not beneficial (Bien et al., 2009; Cross et al., 2013). Here an MEG approach was used to validate these results. The behavioural results from Experiments 3 and 4 were replicated in the present experiment. The sS-R task revealed a BCy effect and the sOS-R task showed a R-BCy effect. The R-BCy effect in the sOS-R task has been replicated in all the experiments in the present study, which shows the reliability of the result. Therefore, the behavioural evidence strongly supports the idea that the processing of task-irrelevant biological cues is influenced by task instructions. In turn, no direct S-R mapping from observed to executed actions should exist for biological cues. However, since the behavioural results only provide indirect evidence about neural processes, this MEG experiment was used to validate the behavioural findings. Importantly, the results of the present study will later be compared to the neural network employed during automatic spatial cueing to answer the question, if humans have developed a unique neural network to process biological stimuli (e.g. a MN system). Since no study has assessed automatic imitation in an S-R paradigm using MEG or EEG, the present study provides the pioneering work in this field. As in Experiment 5, the effect of theta, alpha and beta bands will be discussed separately. However, it is important to keep in mind that neural processes interact to elicit the appropriate behaviour. Most frequency bands did not reveal significant differences between conditions in the sOS-R task. Therefore, most of the discussion will concentrate on the sS-R task.

5.4.1 Biological response-conflict and theta band changes

The sS-R task did not reveal any significant neural clusters in the theta band. Only a negative cluster, which was not statistically significant was found in the left S1 and M1.

This was caused by stronger synchronization in the biologically-congruent in comparison to the biologically-incongruent condition. Since more theta synchronization was found in the biologically-congruent condition where no response-conflict was present, it can be concluded that task-irrelevant biological cues did not trigger conflict induced medial theta synchronization. Medial-frontal theta synchronization is accepted as an indicator of top-down control (Cavanagh & Frank, 2014). The absence of such neural activation during biological response-conflict shows that biological S-R mappings are not guided by top-down control mechanisms such as the spatial equivalent.

5.4.2 Biological response-conflict and alpha band changes

The source localization in the alpha band revealed a neural cluster in visual areas and in the AG located in the IPL. Between 280 to 800 ms more desynchronization was observed in the biologically-incongruent in comparison to the biologically-congruent condition. The IPL has often been related to automatic imitation (Brass et al., 2001, 2005; Mengotti et al., 2012) and to MN activity (Iacoboni, 2005). However, since the IPL showed increased activity during biologically-incongruent trials, the activity cannot be attributed to mirroring. MNs should show increased activity when mirroring is beneficial, that is when the observed action is directly mapped onto the observer's motor system, and not when this should be avoided in the biologically-incongruent condition.

Alternatively, increased alpha desynchronization in posterior areas is related to attention allocation (Händel et al., 2011). Specifically, the AG supports shifts in attention to salient stimulus features (Gottlieb, 2007). Further, the AG is activated when external stimuli are integrated with internal spatial representations to match the response to an observed spatial stimulus (Sack, 2009). It has been shown that alpha desynchronization in posterior regions increases the more cognitive effort is allocated to task completion (Gevins, Smith, McEvoy, & Yu, 1997). Therefore, it is not surprising that increased alpha desynchronization predicts task success.(Lansing et al., 1959; Klimesch & W, 1997). This could also have been the case in the present study, since increased alpha desynchroniza-

tion in the biologically-incongruent condition in comparison to the biologically-congruent condition decreased the automatic imitation effect. Hence, it is likely that more posterior alpha desynchronization in the biologically-incongruent condition either improved performance (sped-up RTs), or too little alpha desynchronization in the biologically-congruent condition worsened performance (slowed down responding).

5.4.3 Biological response-conflict and beta band changes

The beta band revealed a source incorporating the left SMG, PO, vPMC and FEF. Whereas the left PO, vPMC and SMG are part of the core MN system (Molenberghs et al., 2012; Kilner & Lemon, 2013), the FEF is important for the coordination of visual attention by controlling gaze shifts (Olk, Chang, Kingstone, & Ro, 2005). For example, the FEF controls visual attention to an upcoming stimulus by regulating inferior parietal sulcus (IPS) activity via top-down control mechanisms (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008). More interestingly, FEF activity is crucial for dealing with response-conflict during a Simon-like task and double-pulse TMS to the FEF during a Simon paradigm suppresses the Simon effect (Bardi, Kanai, Mapelli, & Walsh, 2012). The present study found more beta desynchronization in the biologically-incongruent in comparison to biologically-congruent condition in the FEF. Hence, it is likely that beta desynchronization in the biologically-incongruent condition is the neural mechanism by which visual attention to the relevant stimulus characteristics is secured. Since S-R mappings in the biologically-congruent conditions are guided by learned long-term S-R associations, responses on the respective trials should not require as much guidance from cognitive processes related to visual attention, which could explain the difference in beta desynchronization between the biologically-congruent and biologically-incongruent conditions in the FEF.

However, more interesting for the current study was that the significant cluster in the beta band reached into well-known MN areas such as the left PO, vPMC and SMG. As in the FEF, greater beta desynchronization during biologically-incongruent in comparison to

biologically-congruent trials was revealed. Interestingly, this neural effect was negatively correlated with the behavioural BCy effect: The more the beta band desynchronized in the biologically-incongruent in comparison to biologically-congruent condition, the greater the behavioural automatic imitation effect. Hence, beta desynchronization in MN areas during response-conflict is important for the automatic imitation effect. These results are in line with previous findings that areas within the IFG (e.g OP or vPMC) are important for automatic imitation. Catmur et al (2009) found that the disruption of the left IFG with TMS abolishes the automatic imitation effect. fMRI studies have also reported that activity in the MFG and the IFG is associated with the inhibition of automatic imitation on biologically-incongruent trials (Brass et al., 2005; Cross et al., 2013). The present study supports the results that areas within the MFG and IFG are crucial when controlling automatic imitation during biologically-incongruent trials (See: Discussion - Experiment 5 and 6 for more detail). However, it also adds new evidence, that beta band oscillations drive the connection between fronto-parietal activity and the control of automatic imitation.

Koelwijn et al. (2008) have presented the only study which reports increased beta desynchronization during perceived conflict. Participants executed and observed actions, which were either correct or erroneous. When observing movements the beta frequency desynchronized more in parietal and central areas during error trials than during non-error trials. In other words, more beta desynchronization was revealed when the participants observed an action, which conflicted their knowledge of a correct response. It was suggested that the beta oscillations in sensory and motor cortices were involved in stimulus evaluation. In line with this interpretation, the present results would suggest that beta desynchronization in the fronto-parietal network is associated with the violation of the natural 'expectation' to perform an imitative response. The more the expectation is violated in the biologically-incongruent in comparison to the biologically-congruent condition, the greater the difference in beta band desynchronization between conditions and the greater the behavioural BCy effect.

Importantly the beta band was the only frequency, which showed an effect in the sOS-R task. A significant cluster was found in the left S1, M1, SPL and VAA. Here beta desynchronized more during biologically-congruent in comparison to biologically-incongruent trials. The effect was observed during the post-movement beta rebound, which is an indicator of post-response neural inhibition (Zaepffel et al., 2013; Kilavik et al., 2013). Therefore, the effect was not related to 'online' conflict management but to post-response mechanisms.

In all, the effects of the present study have shown that BCy is mediated by two mechanisms. First, alpha desynchronization in visual and parietal areas is important to resolve the response-conflict created by the biologically-incongruent task-irrelevant cue. Secondly, beta desynchronization in the left IFG and adjacent areas is associated with increased RTs in the biologically-incongruent condition in comparison to biologically-congruent condition and thereby could be crucial when automatic imitation needs to be inhibited. Unfortunately, no effects were revealed in the sOS-R task, which could be attributed to response preparation and logical recording of the biological cue.

5.4.4 Consious spatial cueing and counter-Cueing

The present study also measured differences in conscious spatial cueing and counter-spatial cueing. The behavioural results replicated the effects observed in Experiments 1 and 2 and revealed faster responses during conscious spatial cueing (sS-R task) in comparison to conscious spatial counter-cueing (sOS-R task). Frontal theta synchronized more during action preparation in comparison to baseline in the sS-R and sOS-R task. Frontal theta synchronization has often been observed during response preparation and it is usually stronger when the response requires more effort (Cavanagh & Frank, 2014).

The sS-R and sOS-R tasks also revealed similar effects in the alpha band. The alpha frequency desynchronized in parietal and visual areas during action preparation in comparison to rest. These effects are likely related to increased attention during response preparation in comparison to rest (Händel et al., 2011). The activity was slightly later-

alized to the right hemisphere. This is surprising, since the responses were made with the right hand, which should have triggered increased alpha desynchronization in the left hemisphere (Lange, Pavlidou, & Schnitzler, 2015).

The beta band also showed very similar activity pattern in the sS-R and sOS-R tasks. In comparison to rest, the beta band showed increased desynchronization in the left M1, bilateral parietal and visual areas. Since the effect is lateralized to the left M1, the effect is showing pre-movement related beta desynchronization, which is important to generate voluntary motor responses (Zaepffel et al., 2013). In all, conscious spatial cueing and counter-cueing revealed neural activities related to response execution and increased attention. No effect could be related to the nature of the imperative spatial stimulus.

5.5 Discussion - Experiment 5 and 6

5.5.1 BCy and SCy Effects

The present MEG studies were set-up to validate the behavioral conclusion from Experiments 1 to 4 that task irrelevant spatial and biological stimuli are processed alike in accordance with the single-route model of Sauser and Billard (Sauser & Billard, 2006). Accordingly, learned S-R mappings should take place in the PPC and be altered by input from the PFC to incorporate the response rule determined by the task instructions. The key here is that spatial and biological task-irrelevant stimuli are both processed depending on the experimental task. Whereas, this has long been accepted for spatial stimuli, there is now also increasing evidence suggesting that the processing of biological stimuli depend on the intentions of the participants and the context in which the biological stimuli are presented (Iacoboni, 2005; Amoruso & Urgesi, 2016; Wurm & Schubotz, 2012).

The present study examined theta, alpha and beta frequencies while SCy/R-SCy and BCy/R-BCy effects were elicited. Whereas automatic spatial cueing has repeatedly evoked frontal theta synchronization (Cohen, 2008; Cohen et al., 2013), conscious imitation has been associated with changes in alpha and beta bands in sensorimotor areas (Sebastiani et al., 2014; Babiloni et al., 2002). The study only assessed the movement preparation period, since it was of interest to find the neural correlates, which facilitated or interfered with the executed actions. Unfortunately, the OS-R tasks did not reveal any significant neural differences between congruent and incongruent conditions during movement preparation. Therefore, much of the discussion will focus on the effects in the S-R tasks.

5.5.2 Biological and spatial response-conflict and theta band changes

Spatial response conflict triggered frontal theta synchronization. An effect, which has been shown in previous studies (Cohen et al., 2008; Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). Frontal theta synchronization increases top-down control processes to execute the correct response (Cohen & Ridderinkhof, 2013; Phillips et al., 2014). The effect is usually

observed when responding is difficult (Jensen & Tesche, 2002). Previously the effect has only been shown using bimanual responses (Cohen et al., 2008; Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). The present study showed that frontal theta synchronization can also be evoked when unimanual responses and biological imperative cues are used. Hence, conflict related theta synchronization is a stable neural mechanism, which likely helps to execute the correct response during spatial response-conflict (Cohen & Ridderinkhof, 2013; Phillips et al., 2014). Seeing that frontal theta synchronization is triggered in a wide variety of situations involving conflict (See, General Introduction and Introduction - Experiment 5), it is surprising that biological response-conflict did not show similar neural activity. Instead a tendency in the opposite direction (increased synchronization in the biologically-congruent in comparison to biologically-incongruent condition) was observed in the left S1 and M1. This dissociates response inhibition triggered by spatial in comparison to biological task-irrelevant cues and shows that these stimuli might be processed in different neural networks.

5.5.3 Biological and spatial response-conflict and alpha band changes

Alpha desynchronizes when an area becomes increasingly active (Klimesch, 2012). SCy and BCy effects both exhibited significant changes in the alpha band. However, the locations were different. Spatial cueing revealed an effect in the CN. This effect was linked to cautious and slow responding when spatial response-conflict was encountered, which enabled the participants to execute the correct rule-bound action (Shadmehr & Holcomb, 1999; C.-s. R. Li et al., 2008; MacDonald et al., 2011). This was stressed by the correlation between the neural and behavioral data, showing that the behavioral SCy effect increased the more alpha desynchronized in the biologically-incongruent in comparison to the biologically-congruent condition (See Discussion - Experiment 5)[29].

Biological cues revealed a classical alpha signature in posterior areas (right V1, left AG and LG), which was attributed to increased attention allocation on biologically-

[29]Importantly, the correlation does not show whether CN activity caused the behavioral changes. Therefore the relationship between neural and behavioral data only shows an association.

incongruent trials (Klimesch & W, 1997; Händel et al., 2011). Increased alpha desynchronization during biologically-incongruent trials in comparison to biologically-congruent trials was associated with a smaller automatic imitation effect. This was not surprising, since alpha desynchronization predicts tasks success (Lansing et al., 1959; Nenert, Viswanathan, Dubuc, & Visscher, 2012). Accordingly, it is likely that increased desynchronization during biologically-incongruent trials enhanced performance on these trials and thereby decreased the behavioral differences between conditions.

All in all, SCy and BCy effects revealed changes in the alpha range, which were related to 'online' conflict control. However, whereas the CN likely controlled responding during spatially-incongruent trials, posterior areas were activated when overcoming biological response-conflict. The results provide evidence that the alpha band is utilized differently to process spatial and biological task-irrelevant stimuli, which again supports the idea that spatial and biological stimuli are processed in different neural networks. Importantly, the analysis in the biological and spatial tasks used slightly different alpha bands, which could contribute to the differences between the observed results. The alpha band often changes between people. Therefore, it would be beneficial to use a within-subject design to directly compare the neural correlates during sS-R and bS-R tasks within the same individuals (Klimesch, Schimke, & Pfurtscheller, 1993).

5.5.4 Biological and spatial response-conflict and beta band changes

Lastly, the SCy manipulation did not evoke any effect in the beta band. The observed frequency pattern was clearly limited to lower frequency bands in the bS-R task. On the other hand, BCy manipulations revealed a significant effect in the beta band in the FEF known for its importance during visual attention and response conflict (Olk et al., 2005; Bardi et al., 2012). But more importantly the classical MN system (left IFG consisting of the PO and vPMC) was also affected.

Interestingly, the IFG (bilateral) shows repetition suppression (See, General Introduction) when participants observe a movement, which was previously executed and vice

versa (Press, Weiskopf, & Kilner, 2012). Therefore, neurons in the IFG are equipped with mirroring properties. Further, disturbing the left IFG with TMS eliminates the automatic imitation effect (Catmur et al., 2009) and, hence, shows a causal relationship between the activity of a MN area and the automatic imitation effect. The present study shows that beta oscillations in the left IFG and MFG likely mediate such changes during automatic imitation. Beta desynchronization in sensory and motor areas is related to the violation of learned behavior, which also happens during biologically-incongruent trials (Koelewijn et al., 2008). Further, the left IFG is gating the imitative response, to ensure that imitation is displayed when appropriate (Bien et al., 2009)(See, Introduction - Experiment 6). Hence, it is interesting that the present study observed an increased behavioral BCy effect the more the beta band desynchronized in the biologically-incongruent in comparison to the biologically-congruent condition. If the left IFG is the gate-keeper for automatic imitation and beta desynchronization mediates this effect, increased beta desynchronization should be observed whenever gate-keeping is useful: in the biologically-incongruent condition when learned behavior needs to be controlled. Further, the more effort is put into the inhibition of automatic imitation during biologically-incongruent in comparison to biologically-congruent trials, the more response interference would be expected in the former in comparison to the latter. This would in turn increase the automatic imitation effect.

However, since the present study did not show any causal effects, more research is needed to investigate the link between beta desynchronization and mirroring. For example, one could use beta entrainment over the left IFG before participants engage in automatic imitation to observe the direct causal relationship between beta activity in the left IFG and the automatic imitation effect.

The link between beta oscillations and the behavioral BCy effect highlights another important aspect of mirroring. Many studies have measured mu activity, which is created by an interplay of alpha and beta frequencies (Hari et al., 1998), using a single electrode approach and have shown increased mu activity during imitation (Bernier et al., 2007;

Désy & Lepage, 2013). By only analyzing a single electrode alpha and beta frequencies can interact without actually stemming from the same areas. This could have created the mu signature during imitation. Hence, it is strongly suggested to use a whole brain approach when assessing alpha (mu) and beta frequencies during imitation instead of relying on a single electrode.

Previous MEG and fMRI studies have questioned whether the biological nature of a stimulus evokes MN activity by showing that a non-biological stimulus elicits mirroring mechanisms in an observer as well, whenever the stimulus is moving in a human-like manner (Catmur & Heyes, 2013; Engel, Burke, Fiehler, Bien, & Rösler, 2008). However, the current study clearly shows that the biological nature of the task-irrelevant stimulus and its congruency with the performed action affect the MN network differently than equivalent manipulations with spatial stimuli.

5.5.5 Spatial and biological response-conflict in OS-R tasks

The OS-R tasks did not show any significant activity, which could be attributed to stimulus congruency during action preparation. The effect in the beta band found in the sOS-R task was observed during post movement beta re-synchronization. Hence, it could not be attributed to action preparation. However, the visual inspection of the sensor level data in the bOS-R and sOS-R tasks (Experiment 5 and 6) showed an opposite pattern in alpha and beta [30] frequencies compared to the respective S-R tasks. In the OS-R tasks posterior alpha and beta frequencies desynchronized more in the congruent in comparison to the incongruent conditions. This pattern was reversed in the S-R tasks. This could indicate that more effort was required in the congruent condition in the OS-R tasks whereas the incongruent condition was more difficult in the S-R tasks (Gola et al., 2013; Siegel et al., 2008). Such neural patterns can provide insights into the logical recoding of S-R mappings applied to the task-irrelevant stimuli. A previous study found that frontal theta synchronization could be used to study the neural correlates of logical recoding (Cao et

[30] Clear beta signatures were only observed in the spatial tasks in Experiment 6

al., 2017). Here it is suggested that posterior alpha and beta frequencies could be provide valuable insights as well.

5.5.6 Conscious imitation and spatial cueing

The present studies also measured the neural correlates during conscious imitation and spatial cueing. The observed effects in the theta, alpha and beta bands were very similar across tasks (SR/OS-R) and stimuli (Spatial/Biological). The theta band showed frontal synchronization during action preparation in comparison to rest in the sS-R, ,sOS-R and bS-R tasks. This was hypothesized since frontal theta synchronization is associated with increased cognitive control and is therefore, beneficial for successful task completion (Maurer et al., 2015). Why no frontal theta synchronization was found in the bOS-R task is questionable. In general, biological stimuli induce less frontal theta synchronization than spatial stimuli (Urgen et al., 2013). Further, reaction times during the bOS-R task were the longest and, hence, there was more spread in the data. This could have decreased the signal to noise ratio and thus, eliminated the effect in the theta band.

The alpha and beta bands revealed increased desynchronization in medial and posterior areas during action preparation in comparison to rest in all tasks. These neural signatures were related to motor planning and visuo-motor attention (Jenkinson & Brown, 2011) and likely unrelated to the nature of the imperative stimuli. Conscious imitation did not evoke any activity, which was attributed to MN activity. This shows that conscious response paradigms indeed shadow the effects revealed when examining the neural effects of implicit spatial and biological cueing.

5.6 Conclusion - Experiment 5 and 6

The comparison between the neural correlates of automatic imitation and its spatial equivalent has shown that the biological nature of the task-irrelevant stimulus indeed determines which cognitive network processes the S-R mapping. Experiment 6 found evidence the MN areas are used to process biological S-R mappings. Instead Experiment 5 showed

that task-irrelevant spatial stimuli activate areas, which are related to cognitive and response control (Shadmehr & Holcomb, 1999; C.-s. R. Li et al., 2008). Experiments 5 and 6 therefore suggest that biological and spatial task-irrelevant stimuli are processed in a direct-matching model (Sauser & Billard, 2006). However, this does not mean that observed biological stimuli are always directly mirrored to elicit imitation. In all experiments of the present study a R-BCy effect was found in the sOS-R task, which clearly shows that biological S-R mappings are influenced by task instructions. Therefore, it is likely that biological and spatial stimuli are processed in distinct cognitive routes, but that both routes are influenced by top-down mechanisms, which take the task instructions into account.

6 Chapter 6

6.1 General Discussion

6.1.1 Behavioral SCy and BCy effects

The present study aimed to understand whether spatial and biological stimuli are processed alike or whether humans have evolved a neural mirroring mechanism to process biological stimuli specifically.

Although many behavioural studies have tried to find differences between the processing of spatial and biological stimuli, these studies have produced very inconclusive results. As pointed out in the General Introduction, some studies have shown that people react faster to biological than to spatial cues (Jonas et al., 2007; Press et al., 2005), or that BCy effects are larger than SCy effects (Brass et al., 2001, 2005). Others have found no benefits when processing biological in comparison to spatial stimuli (Jansson et al., 2007; Gowen et al., 2010) or even better task performance when reacting to spatial in comparison to biological cues (Van Elk et al., 2011; Newman-Norlund, 2010). Due to these contradicting results, it has been difficult to conclude whether biological S-R contingencies indeed have evolved differently than their spatial equivalents. The limitations often seen in studies comparing SCy and BCy effects further complicated the differentiation between the processing of spatial and biological stimuli (See, Introduction - Experiment 3 and 4).

Since it has been difficult to find any conclusive behavioural effects using S-R tasks, Sauser and Billard (2006) proposed using OS-R tasks. In such tasks only spatial task-irrelevant cues would be affected by logical recoding, if biological cues were processed in a direct-matching pathway. (Sauser & Billard, 2006).

In the present thesis, 6 Experiments have been presented, which used S-R and OS-R tasks to measure automatic imitation and its spatial equivalent. All behavioural studies revealed very similar behavioral results for task-irrelevant biological and spatial stimuli. Regardless of stimulus type, a congruency effect was elicited in the S-R tasks, and a reversed congruency effect was found in the OS-R tasks. This pattern was replicated in

the error rate analysis, showing increased errors in the incongruent in comparison to the congruent conditions in the S-R tasks and a reversed pattern in the OS-R tasks.

Task-irrelevant spatial stimuli have repeatedly triggered SCy and R-SCy effects in S-R and OS-R tasks respectively (Proctor, 2011). These results have been interpreted in accordance with the dimensional overlap and the action-suppression models described in the General Introduction and the Introduction to Experiment 1 and 2. The button line is that the learned S-R mapping is guided by long-term S-R associations, which can be controlled by more deliberate short-term S-R associations so that logical recoding of the task-irrelevant stimulus can take place (R. K. Ridderinkhof, 2002).

Task-irrelevant biological stimuli also exhibit very stable automatic imitation effects in S-R paradigms (Heyes, 2011). However, until now biological task-irrelevant stimuli were thought not to elicit R-BCy effects in OS-R tasks, since the observed stimuli were directly mirrored onto the observer's motor system to trigger imitation (Bertenthal et al., 2006; Boyer et al., 2009, 2012). Hence, facilitation of the biologically-congruent response should occur regardless of the task. The discovery of the MN system supported this theory and led many researchers to assume that the unique neural process underlying automatic imitation was found (Rizzolatti & Craighero, 2004; Longo, Kosobud, & Bertenthal, 2008). This was also supported by the behavioural study of Boyer et al. (2012), who did not find a R-BCy effect in the sOS-R task. In contrast, the present study found a R-BCy effect throughout. Suggesting that biological task-irrelevant stimuli are influenced by logical recoding and, therefore, processed similarly to spatial task-irrelevant stimuli (Hedge and Marsh, 1975). Based on the single-route model of Sauser and Billard (2006), task-irrelevant S-R mapping occurs in the PPC. Under normal circumstances, the learned S-R associations are used to select the response. However, in the OS-R task, the PFC encodes the task rules defined by the task instructions and incorporates them into the S-R mapping. This alters the S-R mapping in favour of the incongruent response. This process is relatively slow, but strengthens over time. (R. K. Ridderinkhof, 2002).

As outlined in the Discussion of Experiment 1 to 4, spatial and biological S-R map-

pings are learned by repeated exposure according to the ASL or the ideomotor theory (James, 1890; Press et al., 2011). Hence, the more a person has been exposed to an S-R mapping the greater the associated congruency effect. This is shown by TMS studies revealing increased activity in muscles, which are used in an observed action (Fadiga et al., 1995; Catmur et al., 2007). However, after training during which participants execute an incompatible response to a biological stimulus, observation of this stimulus triggers increased activation in muscles used for the incompatible action (Catmur et al., 2007). Hence, the favoured motor response is altered with training, which suggests that the link between observed and executed movements is learned.

Throughout this thesis, it has been reasoned that the discrepancies between the study of Boyer et al. (2012) and Experiments 3,4 and 6 likely occurred because of the differences in the experimental set-ups. We suggested that variations in the screen refresh rate could have altered the observed effects, if the affected trials were not detected and excluded from the analysis. Further, the usage of a between-subject design in the study of Boyer et al. (2012) lowered the internal validity of their results, since a different group of participants performed the spatial and biological tasks. The present studies, therefore, used within-subject design.

6.1.2 Contribution to long-and short-term S-R associations to SCy and BCy effects

The temporal pattern of the congruency and reversed-congruency effects were examined using a distributional analysis (Ratcliff, 1979). According to the dimensional overlap and action-suppression models, automatic long-term S-R associations elicit fast responses, which are influenced by more deliberate processes building up over time (Kornblum et al., 1990; R. K. Ridderinkhof, 2002). Since the deliberate processes evolve slower, the long-term S-R associations (congruent responses) are most prominent for fast RTs. The output of the distributional analyses showed that the task instructions modified the long-term S-R associations in the OS-R tasks, since reversed-congruency effects were revealed

for the fastest RTs onward. Further, the fastest errors in the OS-R and S-R tasks were in line with the congruency and reversed-congruency effects so that participants made more fast errors in favour of the congruent responses in the S-R tasks, and in favour of the incongruent responses in the OS-R tasks. These results show that logical recoding of the long-term S-R associations must have occurred before participants responded, regardless of the cue type.

Since participants responded faster and made fewer errors in S-R in comparison to OS-R tasks, responding according to the learned long-term S-R associations was easier than using newly formed associations. However, these effects involved conscious responding. Therefore, the involved neural processes were not equivalent to mechanisms used for implicit S-R mappings. However, Heyes (2011) suggested that conscious imitation (e.g. bS-R tasks in Experiment 1,2 and 5) draws on similar cognitive processes as automatic imitation (BCy effects in Experiment 3,4 and 6). Therefore, it is likely that the cognitive processes facilitating conscious imitation (bS-R tasks) or inhibiting conscious counter-imitation (bOS-R tasks) are related to the cognitive processes affecting unconscious biological S-R mapping.

Although the behavioural studies provided convincing evidence for the equivalence between spatial and biological cue processing, the behavioural results only give an indirect understanding of the underlying brain mechanisms. Therefore, it was essential to assess the reliability of the results by the use of imaging techniques. Based on the findings of the behavioural studies (Experiment 1 to 4) it was suggested that task-irrelevant spatial and biological stimuli are processed alike in a manner suggested by the ideomotor or the ASL theories (James, 1890; Press et al., 2011). Therefore, no differences in the neural activation during spatial and biological S-R mappings should have occurred. Importantly, these predictions, were solely based on the behavioural results (Experiment 1 to 4) and not in line with imaging studies comparing the neural correlates of the BCy and SCy effects. Many of these studies reveal different neural activation for the processing of task-irrelevant biological and spatial stimuli (Brass et al., 2001, 2005; Bien et al., 2009; Catmur

et al., 2009; Mengotti et al., 2012). Therefore, the behavioural studies were repeated while using MEG. To date, no study has used MEG recordings while comparing BCy and SCy effects using S-R and OS-R paradigms. This is surprising since MEG has an excellent temporal resolution and ,therefore, can estimate the fast-paced processes leading up to automatic imitation while localizing a complex neural network.

6.1.3 The neural correlates of BCy

Only a few studies have compared the neural correlates underlying SCy and BCy effects, and no study has compared the neural correlates of R-SCy and R-BCy effects (Brass et al., 2001, 2005; Bien et al., 2009; Catmur et al., 2009; Mengotti et al., 2012). From the existing experiments, it is evident that the left IFG is vital for automatic imitation but not for SCy effects. Evidence comes from a TMS study using theta burst stimulation above the left IFG, which eliminated automatic imitation but had no influence on SCy effects (Catmur et al., 2009). Additionally, an fMRI study revealed increased BOLD responses in frontal areas including the posterior parts of the IFG during biologically-incongruent in comparison to biologically-congruent trials (Cross et al., 2013). These results are in line with the findings that the posterior IFG is the gate-keeper for imitative responses, which inhibits their execution if necessary (Bien et al., 2009), and that the left IFG is crucial for evaluating whether biological actions are performed in the correct context (Wurm & Schubotz, 2012). Hence, increased activity in the left IFG is important when controlling imitation so that it is elicited in the correct circumstances.

Lesions in the left IFG have impaired the imitation of finger movements, highlighting its importance for imitation (Goldenberg & Karnath, 2006). Further, Mu desynchronization in the left IFG is related to recognition of human movements in ambiguous, Rorschach stimuli (Pineda et al., 2018), and disrupting the left IFG increases RTs required to recognize emotional expressions, which is accompanied by increases in mu power (Keuken et al., 2011). Based on such results, it was hypothesized that the left IFG is essential for regulating imitation.

In Experiment 6, MEG was recorded while participants engaged in automatic imitation. Here the left MFG and IFG (FEF, PO and vPMC) showed increased beta desynchronization during biologically-incongruent in comparison to biologically-congruent trials. Further, the more the beta band desynchronized in the biologically-incongruent in comparison to the biologically-congruent condition, the greater the behavioural BCy effect. These results confirm the importance of the left IFG during automatic imitation. Here it is hypothesized that the left IFG is crucial when controlling imitation on biologically-incongruent trials. For example, when the tendency to engage in automatic imitation is strong and its inhibition is required (during the biological-incongruent condition), the left IFG gets activated and RTs should increase. If the left IFG is not activated on biologically-congruent trials similarly, which means that participants are reacting automatically, then the automatic imitation effect occurs. Although, the experimental data strongly suggested such relationships between IFG beta desynchronization and behavior, no causal relationship was established. Therefore, it was suggested to use beta entrainment to exactly estimate the role of beta oscillations in the left IFG during automatic imitation (See, Discussion - Experiment 5 to 6).

Although previous studies have shown that mu activity in the left IFG is associated with imitation and action understanding, the current study found significant effects in the beta band. However, since mu activity incorporates alpha and beta components to get its wicked arched shaped form (Hari et al., 1998), the present results are still somewhat in line with previous findings. Anyhow, more research is required to assess the function of the IFG as a gatekeeper for automatic imitation. As mentioned, the cluster ranged into the left SMG in the IPL (Kilner & Lemon, 2013). This area has repeatedly been associated with MN activity. Therefore, it is likely that the revealed cluster was explicitly related to imitation.

Additionally, increased alpha desynchronization was found in posterior areas including the left AG. Since more alpha desynchronization was found in the biologically-incongruent in comparison to biologically-congruent condition, the effect was related to the increased

cognitive effort used to respond correctly during biologically-incongruent trials (Händel et al., 2011). This is especially likely, since the AG is important for adjusting the response to perceived stimuli (Sack, 2009) and increased alpha desynchronization is related to task success (Lansing et al., 1959). Hence, it was expected to observe a smaller automatic imitation effect the more posterior alpha desynchronized in the biologically-incongruent in comparison to the biologically-congruent condition. If posterior alpha desynchronization is an indicator of task success durig S-R mapping, increased alpha desynchronization in the biologically-incongruent in comparison to the biologically-congruent condition would speed up RTs during the former relatively to the latter and thereby decrease the automatic imitation effect.

In sum, BCy effects were guided by two mechanisms. First, increased activity in posterior areas was elicited by biologically-incongruent stimuli to cope with the task demands. Secondly, MN areas showed increased beta desynchronization during biologically-incongruent in comparison to biologically-congruent trials, which was related to the inhibition of automatic imitation. Importantly, the PPC and PFC, which according to the single-route model should guide S-R mapping and logical recoding, were not part of the significant clusters (Sauser & Billard, 2006).

6.1.4 The neural correlates of SCy

In contrast to BCy effects, SCy effects have consistently been related to increased theta synchronization in the medial frontal cortex including the SMA (Nigbur et al., 2011; Cohen & Ridderinkhof, 2013). This effect was replicated in the current study. Although the significant cluster ranged into the SMA, the strongest activity was within the S1. Hence, the results could be related to the integration of sensory and movement information, which could be used to adapt the motor output to the observed stimuli (Borich et al., 2016). Secondly, it could be related to theta synchronization in medial frontal areas seen in other Simon like S-R paradigms (Cohen et al., 2008; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). This has been attributed to increased top-down control processes induced by the

spatial response-conflict (Cohen & Ridderinkhof, 2013; Phillips et al., 2014). Interestingly, no corresponding increase in medial theta power was found for biological response-conflict. This confirms an earlier study showing that the observation of biological stimuli induces less frontal theta synchronization than the observation of spatial stimuli (Urgen et al., 2013).

Lastly, Experiment 5 revealed significant activity in the left CN, which was related to the magnitude of the SCy effect in the bS-R task. The more alpha desynchronized in the spatially-incongruent in comparison to the S-Ct condition, the larger the SCy effect. In Simon tasks increased CN activity has already been found during spatial conflict (Peterson et al., 2002; Liu et al., 2004; Kerns, 2006) and therefore the present study has replicated these previous results from fMRI research. It is likely that alpha desynchronization in the CN pauses responding until the rule-bound behaviour has been executed (Grahn et al., 2008). Hence, the CN could function as a gatekeeper for responding during spatial conflict similar to the role of the left IFG during biological S-R mapping.

The MEG experiments (Experiment 5 to 6) did not find any effects in the OS-R tasks, which could be related to S-R mapping during response preparation, although it was apparent that the posterior alpha and beta activities changed depending on the task (sS-R vs sOS-R and bS-R vs bOS-R). Whereas alpha and beta bands desynchronized more in the incongruent in comparison to congruent conditions in the S-R tasks, this pattern was reversed in the OS-R tasks. Unfortunately, the significant activation found in the beta band in the sOS-R task (Experiment 6) was related to post-response mechanisms.

Although spatial and biological stimuli showed similar behavioural results in Experiment 1-6, Experiment 5 to 6 confirmed previous imaging studies showing differences between the processing of spatial and biological task-irrelevant stimuli. Whereas biological S-R mapping likely occurred in MN areas, spatial stimuli activated areas involved in rule-based behaviour, sensory-motor integration and cognitive control processes. Hence, the results show that different neural networks can evoke similar behavioural patterns induced by spatial and biological stimuli. Despite that the imaging results showed dis-

tinct activity patterns for spatial and biological task-irrelevant stimuli, the results do not suggest that biological stimuli are processed more directly than spatial stimuli. Control processes were likely engaged when participants had to perform an incongruent response and inhibit the congruent response in the S-R tasks, regardless of stimulus type. However, different areas were involved in controlling spatial and biological S-R mappings.

The differences in neural topographies in spatial and biological tasks could be related to the different functions of spatial and biological S-R mappings. As argued in the Discussion of Experiment 1 to 4, automatic imitation promotes social well-being and/or action understanding (Chartrand & Bargh, 1999; Chartrand & Lakin, 2013; Wood et al., 2016). Automatic imitation and motor mimicry have been linked to positive social attitudes (van Baaren et al., 2004; Leighton, Bird, Orsini, & Heyes, 2010). For example, the BCy effect increases if participants are primed by prosocial words in comparison to neutral and anti-social words (Leighton et al., 2010). Similarly, motor mimicry increases when the observer and the actor are befriended and rapport increases between them the more motor mimicry has been shown (Chartrand & Bargh, 1999; Lakin & Chartrand, 2003). Further, activity in the IFG is crucial when recognizing emotions and might also be involved in responding to the revealed emotions correctly (Wood et al., 2016). If perception of biological stimuli (but not spatial stimuli) indeed have these beneficial effects on social behavior, it would only be coherent that biological stimuli activates a unique neural network, which is specialized in social cognition.

6.1.5 Limitations and further directions

Although the use of Boyer et al.'s (2012) paradigm did not include fundamental limitations often seen in the automatic imitation literature (Jansson et al., 2007), there are still factors, which need to be improved in future studies. The most critical problem was that during the first static hand period a right or a left hand was presented for approximately 500 ms on the screen. During these 500 ms, the participants had the chance to predict the upcoming condition. Every time a right hand came on the screen in an S-R task, the trial

was incongruent and when the left hand appeared the trial was congruent. In the OS-R tasks, this pattern was reversed. It has been shown that participants can adjust their performance based on briefly presented stimuli (Bornstein, Leone, & Galley, 1987) and, hence, the first static hand period could influence subsequent S-R mappings by predicting the outcome of the trial. This could have affected the congruency and reversed congruency effects observed in the experiments.

A related problem was the use of specular (mirror images) and anatomical imitation. In the S-R task, all congruent trials used specular stimuli, and all incongruent trials used anatomical stimuli. In the OS-R task, this was reversed. However, specular and anatomical imitation seem to involve different cognitive processes. For example, patients with frontal lobe damage cannot perform anatomical imitation but exhibit no deficit performing specular imitation (Chiavarino, Apperly, & Humphreys, 2007). This is supported by several studies showing that both children and adults prefer specular imitation in comparison to anatomical imitation (Gleissner, Bekkering, & Meltzoff, 2000; Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003) and even MNs are more involved in specular imitation in comparison to anatomical imitation (Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003) . Therefore, the appearance of differing MN activity in the biologically-incongruent vs biologically-congruent conditions in the sS-R task could be induced by the use of specular stimuli in the biologically-congruent condition and anatomical stimuli in the biologically-incongruent condition.

Lastly, the MEG analysis used quite short periods for the beamformers. Although this study only replicated what has been used in other studies assessing Simon effects, this issue still needs to be addressed. MEG frequency resolution improves when increasing the data segment included in the beamformer. Although the present study ensured that the applied data segment included 2 to 3 frequency cycles, the analysis could still be improved by prolonging the time window. Using small time windows decreases the frequency resolution and, therefore, it can become difficult to distinguish which frequency contributed to the effect. By using a different paradigm, which would automatically increase RTs an extended

data segment could be used for the analysis.

The study found convincing evidence that beta desynchronization in MN areas is important for the automatic imitation effect but not for the SCy effect. Since the current MEG studies could not establish a causal relationship between the observed brain activity and the behavioural data, it would be necessary to follow-up using a TMS approach with beta entrainment to the left IFG during bS-R and sS-R tasks as suggested in the Discussion of Experiment 5 and 6. Another question would be why spatial and biological stimuli elicit similar behavioural effects although the stimuli are processed in separate neural networks. Here it would be of interest to assess when the networks switch, to answer the question: how biological does a stimulus need to be, to be processed in MN areas? This is related to the question whether MN activity can be evoked by training. As described above, TMS studies have shown that after counter-imitation training, the presentation of the movement stimulus evokes greater MEPs in the muscles used for counter-imitation in comparison to imitation (Catmur et al., 2007) and stimulating the vPMC (a MN area) before responding strengthens imitation as well as counter-imitation (Catmur, Mars, Rushworth, & Heyes, 2011). Further, training participants to respond to robotic stimuli abolishes the differences between compatibility effects elicited by robotic or human stimuli (Press, Gillmeister, & Heyes, 2007). Future studies need to establish whether training participants to react in an incompatible manner can reverse the neural signature in MN areas seen in the sS-R task of the current thesis. This could further strengthen the hypothesis that automatic imitation is a learned behavior.

6.2 Conclusion

The present study aimed to understand whether spatial and biological stimuli are processed alike or whether humans have evolved a cognitive and neural mirroring mechanism specifically to process biological stimuli. The behavioural results of Experiment 1 to 6 were similar for spatial and biological stimuli, which suggested that long-term S-R associations elicited the congruency effects in the respective S-R tasks. Importantly both

stimulus types were influenced by short-term S-R processes in the OS-R tasks since both tasks revealed reversed congruency effects. Despite the convincing behavioural results that spatial and biological task-irrelevant stimuli are processed alike, the MEG studies (Experiment 5 and 6) revealed conflicting findings. Whereas BCy effects trigger activation in classical MN areas, SCy effects triggered activity in areas related to top-down control and rule-bound behaviour. Although MN areas were uniquely involved in the processing of biological stimuli, biological stimuli were not directly mapped onto the observer's motor system by the pure observation of the sensory information. Instead, the biologically-incongruent response was preferred when participants responded incompatibly to the imperative stimulus. These results should change how we think about MN activity. Instead of understanding activity in MN areas as a compulsive force to imitate, activity in MN areas could be important for controlling imitation as well. This is especially likely since the present study revealed that MN areas could be involved when imitation needs to be inhibited. Hence it is crucial to adopt a more differentiated perspective when understanding and assessing the MN network.

A Appendix 1

A.1 Legend for the single-route and direct-matching models

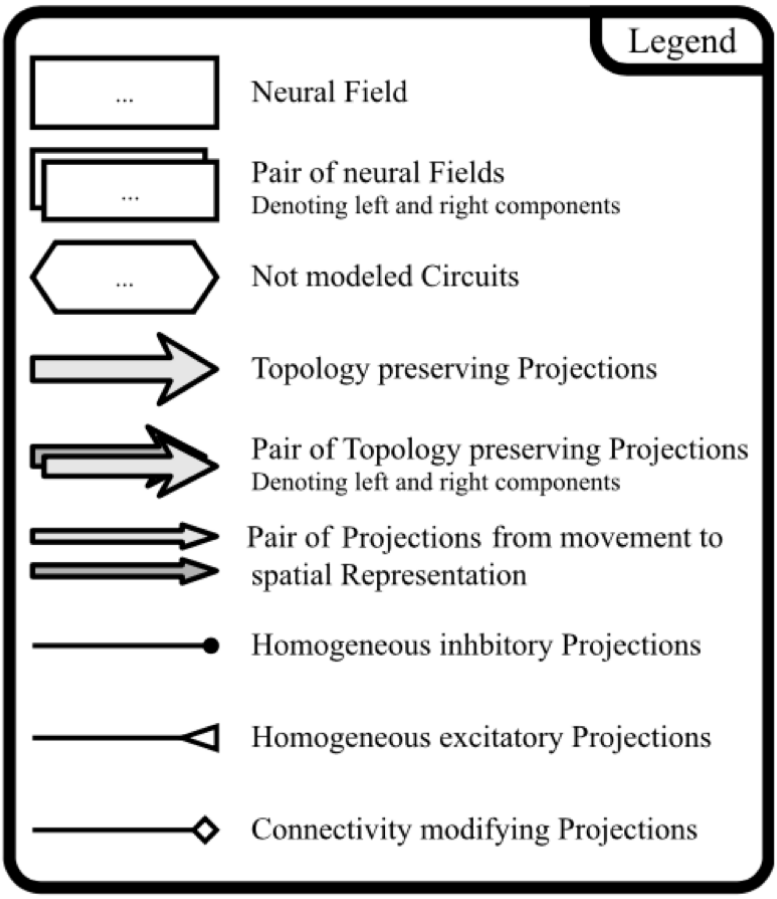


Figure 31: Shows the Legend for the single-route and direct-matching models from Sauser and Billard (2006), which explains the arrows/cognitive routes displayed in the models.

B Appendix 2

B.1 Results outliers

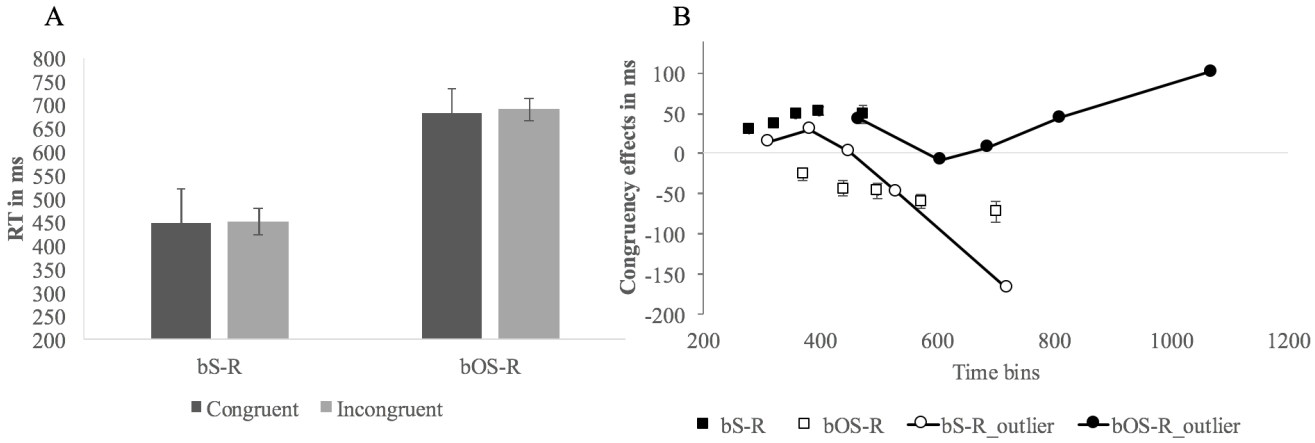


Figure 32: Shows the results from the outliers in Experiment 1. (A) shows the RTs on the y-axis and the task (bS-R/bOS-R) divided into congruent and incongruent conditions. The participants did not reveal a BCy and a R-BCy effect. (B) shows the distributional analysis for the outliers compared with the delta plots for the rest of the 18 participants. It is visible that the outliers revealed a very different pattern in comparison to the rest of the participants

C Appendix 3

No materials were included in the appendix.

D Appendix 4

D.1 Event-related potentials and SCy

The pioneers assessing the neural correlates of the Simon task measured the Lateralized Readiness Potentials (LRP), since it reveals the activation of the motor system before action execution. The LRP is measured over central electrodes (C3 and C4) 160 to 190 ms after stimulus presentation (Mansfield, van der Molen, Falkenstein, & van Boxtel, 2013). It is calculated by subtracting the activity of the hemisphere contralateral to the responding hand from the activity of the hemisphere ipsilateral to the responding hand. During response preparation, the motor cortex desynchronizes with a bias towards the hemisphere contralateral to the moving hand. Therefore, the LRP is positive when performing the mentioned subtraction. However, in a Simon task, the valence of the LRP depends on the task (S-R/OS-R) and the spatial congruency (spatially-congruent, spatially-incongruent stimulus). During the spatially-congruent condition and S-R task, the LRP is positive, which confirms the activation of the stimulus-contralateral hemisphere, which is guiding the congruent response. During the spatially-incongruent condition in the S-R task, the hand ipsilateral to the stimulus is incorrectly triggered by the spatial conflict. Thus, the resulting LRP is negative at the start and returns to positive valence approximately 180 ms after the presentation of the spatial task-irrelevant stimulus (De Jong et al., 1994; Mansfield et al., 2013; Masaki, Takasawa, & Yamazaki, 2000). Based on these results, the neural predisposition underlying the beneficial responses to spatially-congruent stimuli in the S-R task was confirmed. Interestingly the LRP in the spatially-congruent in the OS-R task revealed an unique pattern: Initially the bias towards the spatially-congruent response remained, since more activation was found in the hemisphere contralateral to the stimulus. This was interrupted by an intermediate activation of the ipsilateral hemisphere, which would trigger an spatially-incongruent response, before the stimulus contralateral hemisphere got increasingly active and the correct (congruent) response was executed (Dejong, 1994). This result shows that the automatic tendency to respond to the spatially-

congruent stimulus in the OS-R task did not vanish. Instead, it was interrupted by the re-coding of the S-R association and the intermediate tendency to respond in an spatially-incongruent manner.

Other ERP studies followed confirming the internal bias toward the spatially-congruent response in the S-R task. However, none of them discriminated between congruent and incongruent trials in the OS-R task.

One ERP, which has been measured repeatedly during a Simon-like task is the P300. It occurs approximately 300 ms after stimulus onset over parietal areas (e.g. electrode Pz). Since the latency of the P300 varies with RT, the P300 is related to cognitive timekeeping (Leuthold, 2011). Similarly, in the S-R task the latency of the P300 increases on spatially-incongruent trials in comparison to spatially-congruent trials, since the former on average is associated with longer RTs (Valle-Inclán, 1996; Ma & Shang, 2013; Masaki et al., 2000). Hence, the P300 component is related to the withholding of the response until the conflict has been resolved (Ma and Shang, 2013). Further the positive amplitude of the P300 increase on congruent trials in comparison to incongruent trials in the S-R task, which stresses the relationship between P300 reactivity and cognitive conflict (Zhou, Zhang, Tan, & Han, 2004; Galashan, Wittfoth, Fehr, & Herrmann, 2008). Importantly, the P300 does not show differential effects to spatially-congruent or spatially-incongruent trials in the OS-R task (Valle-Inclán, 1996; Cao et al., 2017). This could indicate that the S-Cy and R-SCy effects rely on different neural processes. In all, these results show that the central parietal cortex is involved in withholding a response during response conflict in the S-R task but not in the OS-R task.

Lastly, the N2 ERP is measured in central electrodes (Cz electrode) as a negative wave at approximately 200 to 350 ms after stimulus onset (Folstein & Van Petten, 2008). The N2 component has repeatedly been assessed in the oddball paradigm. During an oddball paradigm participants react to the same stimulus repeatedly but in-between a deviant stimulus occurs. The RTs and neural processes to this deviant stimulus (oddball) are of interest. The amplitude of the N2 component is larger when the oddball is presented

than when a usual stimulus is on the screen. Hence, the N2 component has been related to the detection of novelty as well as to cognitive control (Folstein & Van Petten, 2008). In the Simon task the N2 component increases in amplitude during spatially-incongruent trials in comparison to spatially-congruent trials in the S-R task (K. Wang et al., 2014; Melara, Wang, Vu, & Proctor, 2008), although not all studies have replicated these results (Mansfield et al., 2013). Currently, only one study has assessed the N2 amplitude in the OS-R task and found no difference between spatially-congruent and spatially-incongruent trials (Cao et al., 2017). Hence, the P300 and N2 component only show differences between spatially-congruent and spatially-incongruent conditions in the S-R task. Interestingly, it has been suggested that the N2 component is carried by the increase in theta power over fronto-central areas during response conflict (Harper, Malone, & Bernat, 2014; Cavanagh & Frank, 2014), a topic which will be outlined in the main text of the Introduction - Experiment 5.

In sum, the insights from LRP studies show that the motor system is biased towards the spatially-congruent response in the S-R and OS-R tasks. However, in the OS-R task there is an additional tendency to respond in a spatially-incongruent manner, which starts after the initial tendency to respond in a congruent fashion. The P300 and N2 components only discriminate between task-irrelevant spatially-congruent and spatially-incongruent stimuli in the S-R but not the OS-R task. Accordingly, central and parietal areas were only associated with spatial conflict processes when the participants were required to map the observed stimulus and the executed response. The present study will not perform any ERP analysis since ERPs are restricted to specific spatial locations. For the current line of studies this is not convenient, since it is of special interest to assess the contribution of mirror neuron areas such as the premotor cortex, pars opercularis, frontal eye fields and inferior parietal cortex, which are not the loci of the mentioned ERPs. Therefore, the present study will focus on time-frequency calculations and more complex neural networks associated with theta, alpha and beta frequencies.

D.2 Between condition analysis comparing action preparation during spatially congruent and incongruent trials in the bS-R task.

The effects of spatial congruency in the beta band: Changes in beta frequency (13-25hz) between spatially-congruent and spatially-incongruent conditions were examined in the bS-R task but did not reveal any significant results. Topoplots of the differences between spatially-congruent and spatially-incongruent conditions in the beta band showed very weak changes. These were further examined by difference TFRs (incongruent-congruent condition) and sensor level statistics, but neither method revealed any clear beta band activity that could be examined further.

D.3 Between condition analysis comparing action preparation during spatially congruent and incongruent trials in the bOS-R task.

The effects of spatial congruency in the theta band: Differences between spatially-congruent and spatially-incongruent conditions in the theta band in the bOS-R task were examined but did not reveal any meaningful results. The topoplots of the differences between spatially-congruent and spatially-incongruent conditions in the theta band showed left central synchronization. However, the corresponding difference TFR and statistical testing did not reveal any visible differences between conditions or any statistically significant results. That is, in contrast to the bS-R task, the bOS-R task did not reveal any conflict induced changes in the theta band.

The effects of spatial congruency in the alpha band: Figure 33 shows the sensor level plots of the differences between spatially-congruent and spatially-incongruent conditions (incongruent-congruent condition) in the alpha band in the bOS-R task. The topoplots of the differences between conditions reveal posterior synchronization throughout the depicted period (0 to 800 ms), and the corresponding difference TFR of the

posterior channels revealed clear alpha synchronization from 0 to 800 ms. This was due to increased desynchronization in the spatially-congruent in comparison to the spatially-incongruent condition. However, no significant sensor or source level results could be found in the alpha band. Interestingly, the bOS-R and the bS-R tasks showed opposite patterns in the difference plots (incongruent-congruent condition) in the alpha band. Whereas the former revealed posterior synchronization the latter revealed posterior desynchronization.

The effects of spatial congruency in the beta band: Figure 33 shows the sensor level plots of the difference between conditions (incongruent-congruent condition) in the beta band in the bOS-R task. The topoplots reveal very similar, but attenuated, topographies as those of the alpha band. The corresponding difference TFR shows increased beta activity before stimulus movement onset until 1000 ms after stimulus movement onset with a small period of desynchronization between 600 to 700 ms. No significant sensor or source level differences between spatially-congruent and spatially-incongruent conditions could be found in the beta band. Overall, the activity pattern was reversed from the bS-R task, in which the difference TFR revealed posterior beta desynchronization.

D.4 Within condition results comparing rest and action preparation periods in the bS-R task

Theta band changes during rest and action preparation:Figure 34 Panel A shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the bS-R task for the theta band. In comparison to a relative baseline corresponding the the rest period, the theta band revealed increased frontal synchronization and posterior desynchronization during action preparation. The time-frequency representation (TFR) with a relative baseline from -500 to -50 ms of left frontal channels shows that the frontal synchronization starts around 250 ms after stimulus movement onset and continues until 750 ms after stimulus movement onset. During decision making tasks, theta in fronto-central areas synchronize as an indicator of working mem-

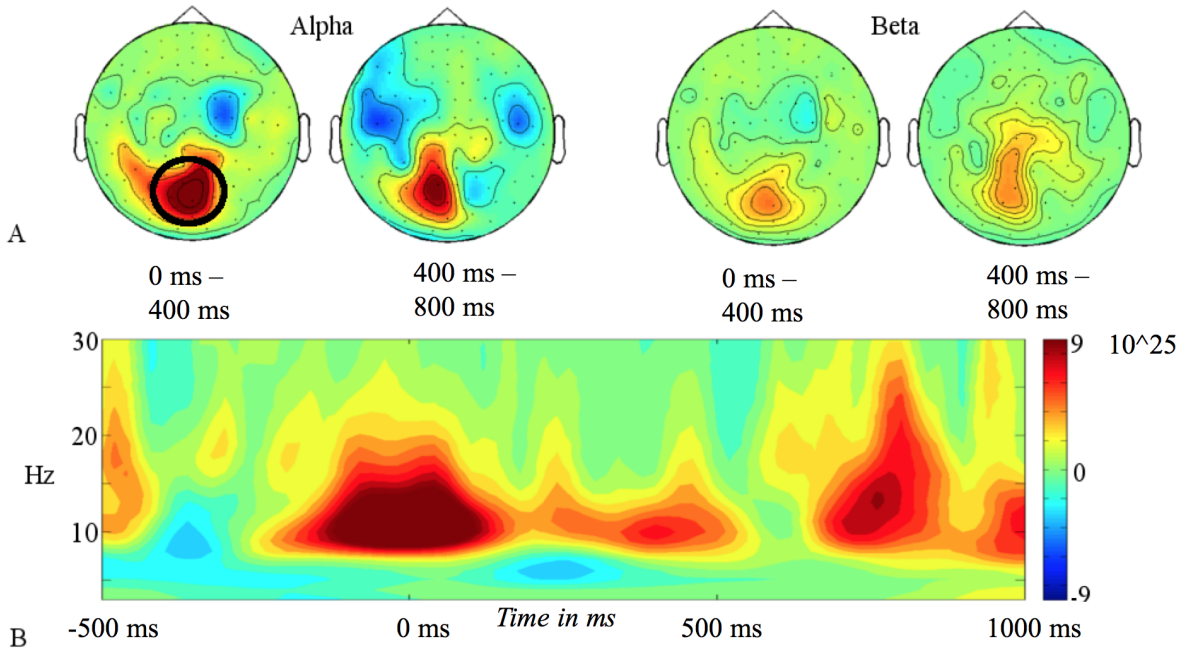


Figure 33: (A) Topoplots of the differences between conditions (incongruent-congruent condition) of the alpha and beta bands from 0 to 400 ms and from 400 to 800 ms in the sOS-R task. The black circle indicates the approximate channels used in the TFR in B. (B) A TFR from posterior channels with a relative baseline between -1000 to -700 ms.

ory engagement (Sauseng, Klimesch, Doppelmayr, Hanslmayr, Schabus, Gruber, 2004). In the present study it is especially of interest to assess processes during response preparation. However, since the theta activity in the sensor level TFR showed later changes it is likely that these are not just related to response preparation but also to working memory processes after responding. A beamformer was set up to localize the differences between rest (-750 to -50 ms) and action (preparation) period (50 to 750 ms; action preparation - rest) in the theta band (4-7 Hz). This revealed a significant negative cluster in the posterior areas with the global minimum in the right cerebellum (MNI 18 -88 -24) and several local minima such as the bilateral lingual gyrus (LG; MNI 35 -80 8; -36 -89 18), bilateral V1 (MNI 18 -97 3; -5 -95 6), right visual association area (VAA; MNI 18 -84 18), right fusiform gyrus (FG; MNI 52 -64 8), right AG (MNI 42 -78 36) and left SPL (MNI 30 -54 54). A virtual electrode placed into the right cerebellum and plotted with a relative baseline from -750 to -50 showed that the activity was centred over the alpha band. Hence, it is likely that the observed activity is an artifact from the alpha frequency. Additionally,

a positive frontal cluster with global maximum in the left temporal pole (TP; MNI -44 0 -32) and local maxima in the left frontopolar cortex (FPC; MNI -12 64 28), left PO (MNI -54 24 24) and left PFC (MNI -42 36 30) was found. A virtual electrode in the left TP and plotted with a relative baseline from -750 to -50 showed weak theta synchronization from approximately 300 ms post movement stimulus onset (Figure 35 Panel A).

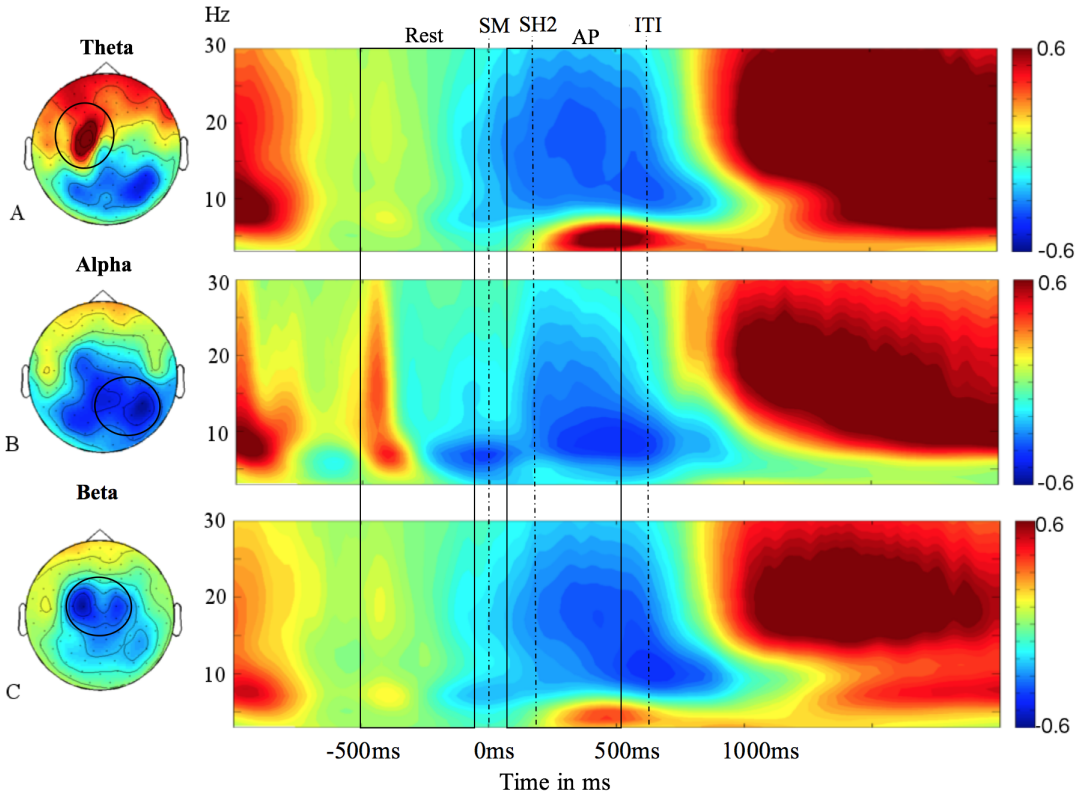


Figure 34: Shows the topoplots of the (A) theta, (B) alpha and (C) beta bands in the bS-R task comparing the rest (-500 to -50 ms) and action preparation (50 to 500 ms) periods (action preparation - rest). A TFR comparing rest and action preparation periods is shown for each frequency band as well. A set of frontal channels was used for the TFR in the theta band (A), a set of posterior channels was used for the TFR in the alpha band (B) and a set of central channels was used for the TFR in the beta band (C). The black circles indicate the approximate location of the chosen channels. All TFRs and topoplots were visualized with a relative baseline corresponding to the rest period (-500 to -50 ms). The solid lines in the TFRs show the rest and action preparation (AP) periods and the dotted lines indicate the onset of the stimulus movement (SM), the second static hand (SH2) and the inter-trial interval (ITI).

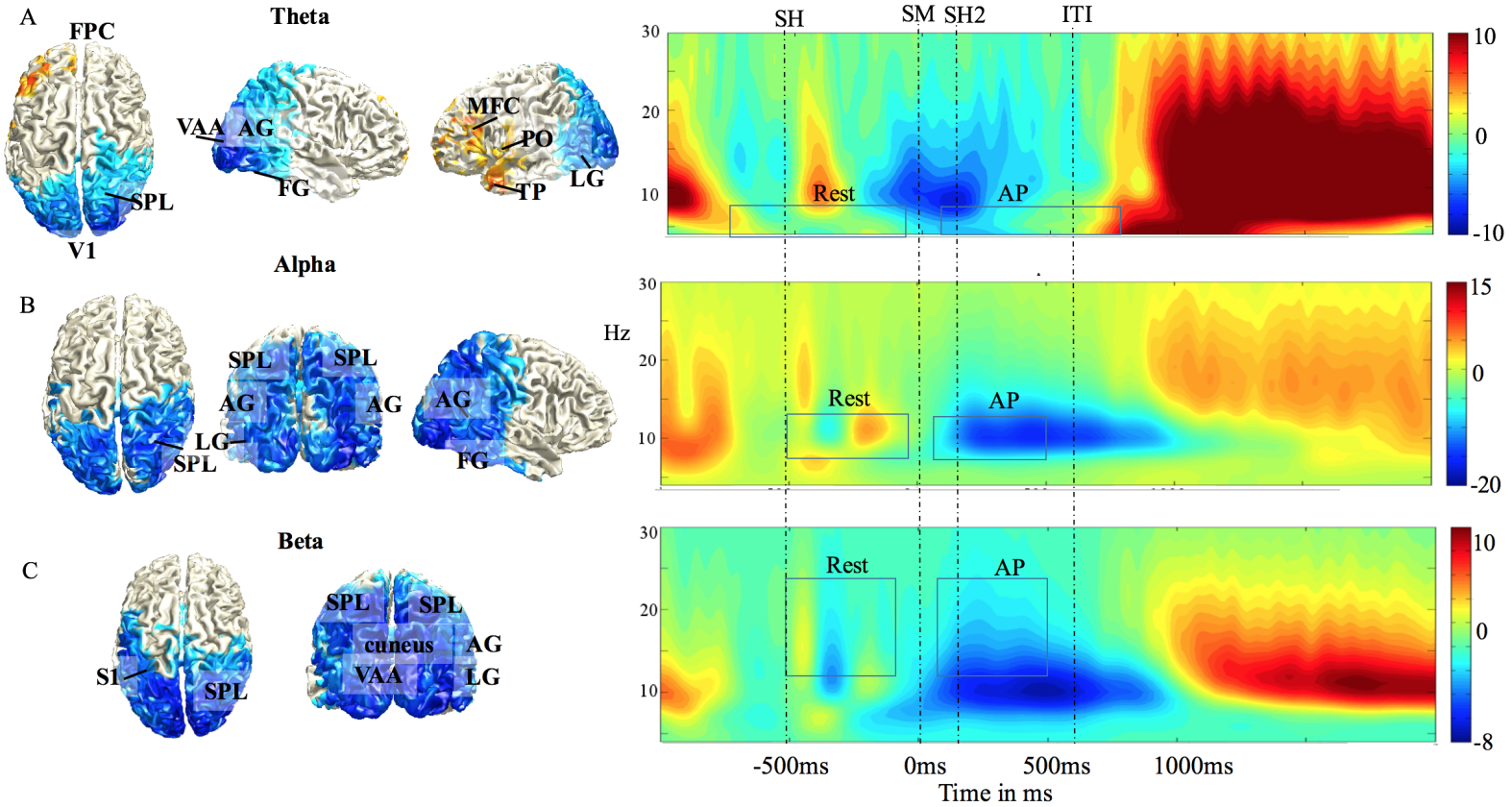


Figure 35: Within-condition source localizations in the bS-R task for (A) theta, (B) alpha and (C) beta bands and the corresponding TFRs of the virtual electrodes placed in the global maximum/minimum of the clusters. The source localization in the theta band used a time window from 50 to 750 ms (action preparation, AP) to include more of the theta band observed in the sensor level TFRs. The rest period (-750 to 50 ms) was chosen accordingly. For the alpha and beta bands similar action preparation (50 to 500 ms) and rest (-500 to -50 ms) periods were chosen. Virtual electrodes in the left PFC (A), the right cerebellum (B) and the left VAA (C) were localized in the theta, alpha and beta bands respectively. The rectangles indicate the rest and action preparation periods (AP) and the dotted lines show the onset of the static hand (SH), the stimulus movement (SM), the second static hand (SH2)and the inter-trial interval (ITI).

Alpha band changes during rest and action preparation: Figure 34 Panel B shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the bS-R task for the alpha (8-12 Hz) band. The topoplots with a relative baseline corresponding to the rest period revealed alpha desynchronization in bilateral posterior channels during the action preparation period in comparison to rest. A TFR of posterior channels with a relative baseline from -500 ms to -50 ms shows desynchronization during the whole period of action preparation (50 to 500 ms). A source localization of the differences in alpha power between rest (-500 to- 50 ms) and action preparation (50 ms to 500 ms; action preparation - rest) revealed a significant negative cluster with global minimum in the right cerebellum (MNI 30 -84 -36) and local minima in the bilateral LG (MNI 28 -72 -8; -36 -78 -12), bilateral AG (MNI 48 -48 18; -48 -66 18), bilateral SPL (MNI 30 -66 60; -18 -66 60) and right FG (MNI 42, -30, -18; Figure 35 Panel B). A virtual electrode in the right cerebellum confirmed that alpha desynchronized more during action preparation in comparison to rest using a relative baseline.

Beta band changes during rest and action preparation: Figure 34 Panel C shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 ms to 500 ms) in the bS-R task for the beta (13-25 Hz) band. The topoplot showed bilateral posterior desynchronization during the action preparation period in comparison to a relative baseline corresponding to the rest period. A TFR of posterior channels with a relative baseline from -500 ms to -50 ms shows greater desynchronization during action preparation in comparison to rest. A source localization of the differences in beta power between action preparation (50 ms to 500 ms) minus rest (-500 to -50 ms) revealed a significant negative cluster with global minimum in the left VAA (MNI -6 -78 30) but several local minima such as the bilateral SPL (MNI 30 -60 60; -12 -60 60), bilateral AG (MNI 54 -48 30; -54 -48 30), bilateral cuneus (MNI 6 -84 36; -6 -84 36) and bilateral V1 (MNI 48 -18 42; -48 -18 42; $p < 0.01$; Figure 35 Panel C). A virtual electrode using a relative baseline and placed in the global minimum of the source cluster showed beta-band desynchronization throughout the action preparation period in comparison to rest (Figure 35 Panel C).

D.5 Within condition results comparing rest and action preparation periods in the bOS-R task

Theta band changes during rest and action preparation: Figure 36 Panel A shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the bOS-R task for the theta (4-7 Hz) band. The topoplot with a relative baseline corresponding to the rest period revealed left frontal synchronization during the action preparation period. A corresponding TFR of left frontal channels with a relative baseline from -500 to -50 ms showed that the synchronization started around 300 ms after stimulus movement onset and continued until 1000 ms. As in the bS-R task the observed frontal changes in the theta band, which could be related to working memory changes during responding (Itthipuripat1, Wessel and Aron, 2013) were found after 300 ms. Hence, it is likely that they are related to changes pre-and post responding.

Nevertheless, a beamformer was set-up to localize these changes in theta band during the action (preparation) period (50 to 750 ms) in comparison to rest (-750 to -50 ms). This revealed a significant negative cluster in posterior areas with a global minimum in the right cerebellum (MNI 12 -84 -19) and local minima in visual areas such as bilateral VAA (MNI 36 -90 6; -18 -84 0), right LG (MNI 42 -84 18) and right cuneus (MNI 42 -80 30 ; 37 Panel A). No frontal positive cluster was found. A virtual electrode in the right cerebellum with a relative baseline from -750 to -50 ms revealed theta desynchronization throughout the action preparation period (37 Panel A). However, the activity was clearly centred over the alpha and not the theta band.

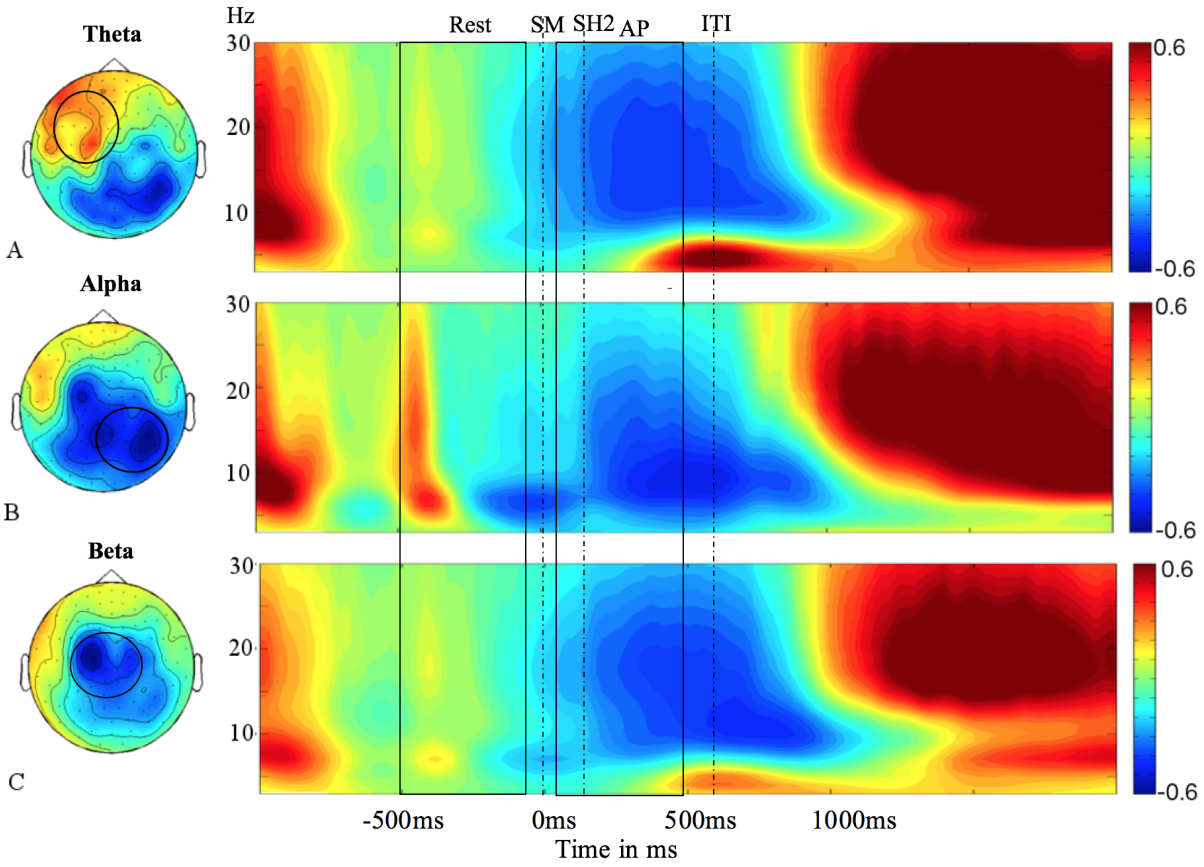


Figure 36: Shows the topoplots of the (A) theta, (B) alpha and (C) beta bands in the bOS-R task comparing the rest (-500 to -50 ms) and action preparation (50 to 500 ms) periods (action preparation - rest). A TFR comparing rest and action preparation periods is shown for each frequency band as well. A set of frontal channels was used for the TFR in the theta band (A), a set of posterior channels was used for the TFR in the alpha band (B) and a set of central channels was used for the TFR in the beta band (C). The black circles indicate the approximate location of the chosen channels. All TFRs and topoplots were visualized with a relative baseline corresponding to the rest period (-500 to -50 ms). The solid lines in the TFRs show the rest and action preparation (AP) periods and the dotted lines indicate the onset of the stimulus movement (SM), the second static hand (SH2) and the inter-trials interval (ITI).

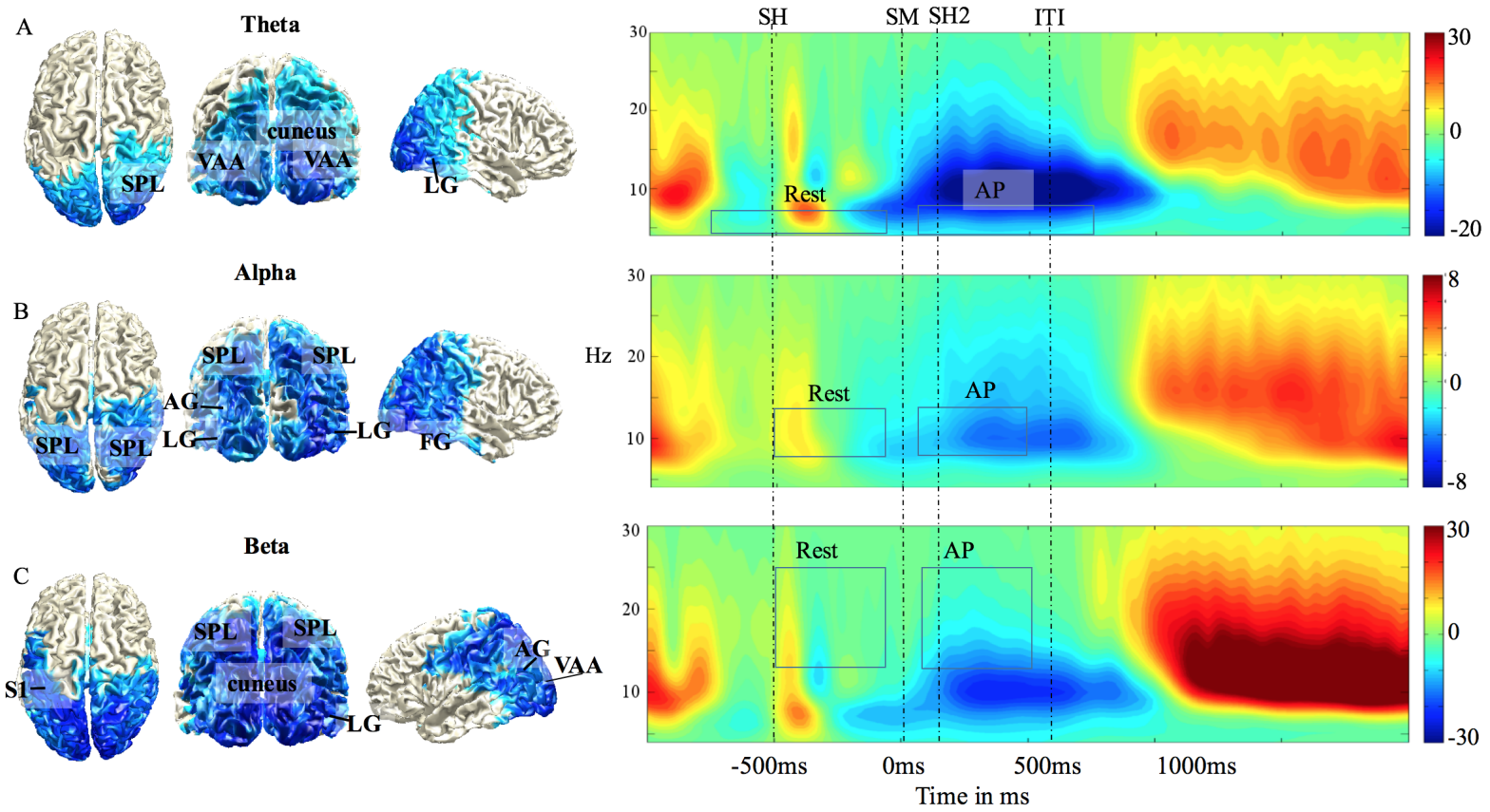


Figure 37: Within-condition source localizations in the bOS-R task for (A) theta, (B) alpha and (C) beta bands and the corresponding TFRs of the virtual electrodes placed in the global minimum of the clusters. The source localization in the theta band used a time window from 50 to 750 ms (action preparation, AP) to include more of the frontal theta synchronization observed in the sensor level TFR. The rest period (-750 to 50 ms) was chosen accordingly. For the alpha and beta bands similar action preparation (50 to 500 ms) and rest (-500 to -50 ms) periods were chosen. Virtual electrodes were placed in the right cerebellum (A), right cerebellum (B) and the left VAA (C) for the theta, alpha and beta bands respectively. The rectangles indicate the rest and action preparation periods (AP) and the dotted lines show the onset of the static hand (SH), the stimulus movement (SM), the second static hand (SH2)and the inter-trial interval (ITI).

Alpha band changes during rest and action preparation:Figure 36 Panel B shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the bOS-R task for the alpha (8-12 Hz) band. The topoplot with a relative baseline corresponding to the rest period revealed desynchronization in central and posterior areas during the action preparation period, which was confirmed in the corresponding TFR of posterior channels. A source localization of the differences in alpha power between rest (-500 to -50 ms) and action preparation (50 to 500 ms; action preparation - rest) revealed a significant negative cluster very similar to the cluster found in the bS-R task with global minimum in the right cerebellum (MNI 36 -84 -36) and local minima in the bilateral LG (MNI 36 -78 12; -36 -78 -12), bilateral AG (MNI 48 -66 18; -48 -66 18), bilateral SPL (30-66 54; -18 -66 60) and right FG (MNI 42, -30, -18). A virtual electrode with a relative baseline and placed in the local minimum of the cluster and confirmed that the source showed increased desynchronization during action preparation in comparison to rest (Figure 37 Panel B).

Beta band changes during rest and action preparation: Figure 36 Panel C shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the bOS-R task for the beta (13-25 Hz) band. The topoplot revealed desynchronization in the central channels during action preparation in comparison to rest using a relative baseline. A corresponding TFR of central channels showed increased desynchronization throughout action preparation in comparison to rest. A source localization of the differences in beta power between rest (-500 to -50 ms) and action preparation (50 to 500 ms; action preparation – rest) revealed a significant negative cluster with global minimum in the left VAA (MNI -6 -78 30) and similar local minima as in the bS-R task such as the bilateral SPL (MNI 30 -60 60; -12 -60 60), left cuneus (MNI -6 -84 36), left S1 (MNI -48 -18 36), right AG (MNI 54 -48 30) and right medial temporal gyrus (MTG; 52 -43 9; Figure 37 Panel C). A virtual electrode using a relative baseline and placed into the left VAA confirmed that the beta band showed increased desynchronization during action preparation in comparison to rest (Figure 37 Panel C).

D.6 Significant differences between conditions in the virtual electrodes - Experiment 5

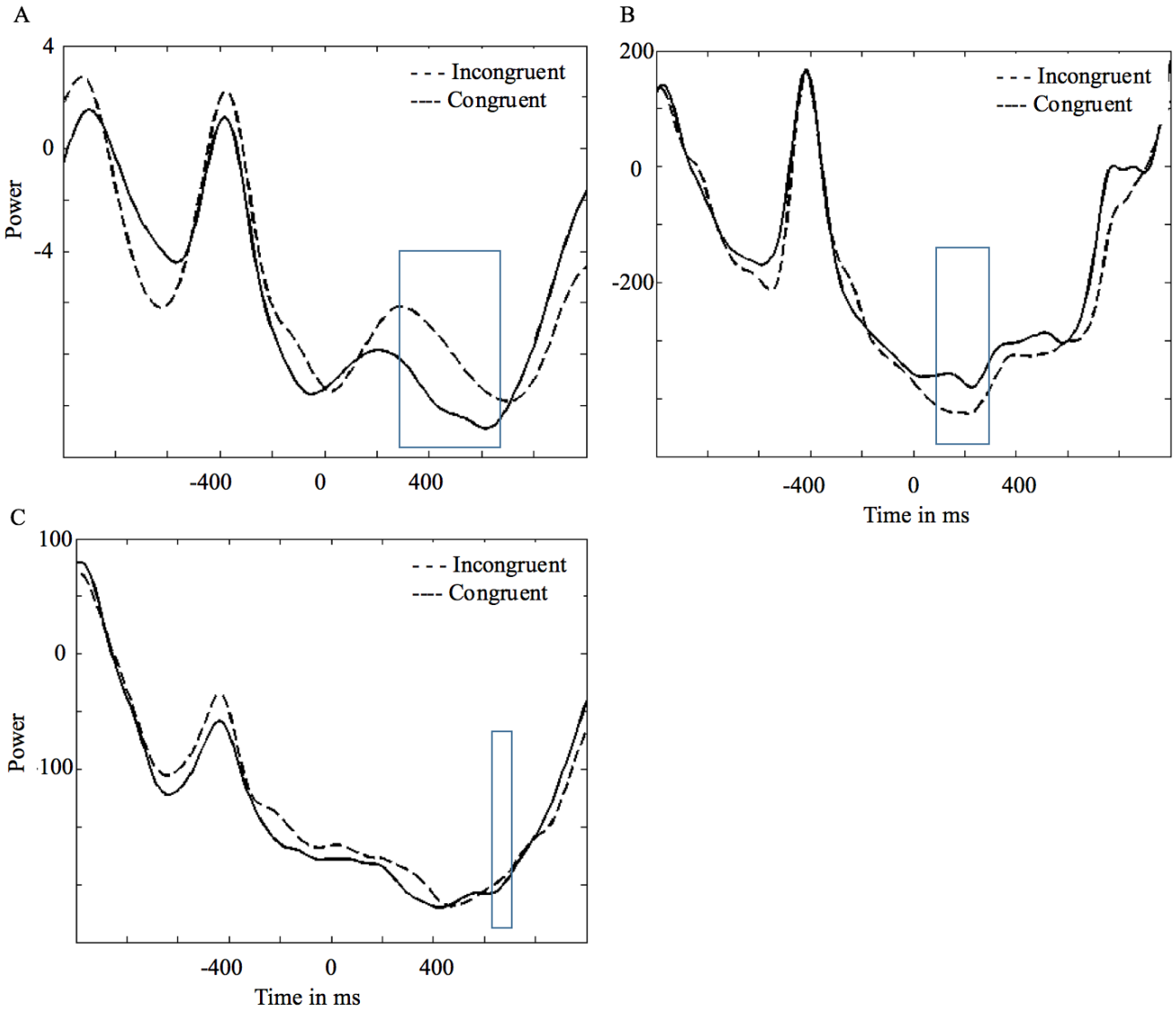


Figure 38: The graphs show the output of the virtual electrode test statistics in the bS-R tasks of Experiment 5. (A) The virtual electrode positioned in the left S1 shows the average theta power over time in the spatially-congruent and spatially-incongruent conditions. The virtual electrodes positioned in the (B) left CN and (C) right LG show the average alpha power over time spatially-congruent and spatially-incongruent conditions. The rectangles indicate the periods where the conditions significantly differed.

D.7 MNI coordinates - Experiment 5

bS-R Theta	MNI
right cerebellum	18 -88 -24
bilateral lingual gyrus	35 -80 8; -36 -89 18
bilateral primary visual cortex	18 -97 3; -5 -95 6
right visual association area	18 -84 18
right fusiform gyrus	52 -64 8
right angular gyrus	42 -78 36
left superior parietal lobule	30 -54 54
the left temporal pole	-44 0 -32
left frontopolar cortex	-12 64 28
left pars opercularis	-54 24 24
left medial frontal cortex	-42 36 30
right primary sensory cortex	12 -36 62
medial supplementary motor area	0 -12 60
left primary motor cortex	-6 -30 75
bS-R Alpha	**MNI**
the right cerrebellum	30 -84 -36
bilateral lingual cortex	28 -72 -8; -36 -78 -12
bilateral angular gyrus	48 -48 18; -48 -66 18
bilateral superior parietal lobule	30 -66 60; -18 -66 60
right fusiform gyrus	42, -30, -18
caudate nucleus	-6 12 0
left fusiform gyrus	-48 -54 -6
right lingual gyrus	12 -66 -5
left lingual gyrus	-30 -72 -12
left superior parietal lobule	-18 -66 48
bS-R Beta	**MNI**
left visual association area	-6 -78 30
bilateral superior parietal lobule	30 -60 60; -12 -60 60
bilateral angular gyrus	54 -48 30; -54 -48 30
bilateral cuneus	6 -84 36; -6 -84 36
bilateral visual primary cortex	48 -18 42; -48 -18 42

Table 4: MNI coordinates bS-R task

bOS-R Theta	MNI
right cerebellum	12 -84 -19
bilateral visual association area	36 -90 6; -18 -84 0
right lingual gyrus	42 -84 18
right cuneus	42 -80 30
bOS-R Alpha	MNI
right cerebellum	36 -84 -36
bilateral lingual gyrus	36 -78 12; -36 -78 -12
bilateral angular gyrus	48 -66 18; -48 -66 18
bilateral superior lobule	30-66 54; -18 -66 60
right fusiform gyrus	42, -30, -18
bOS-R Beta	MNI
left visual association area	-6 -78 30
bilateral superior parietal lobule	30 -60 60; -12 -60 60
left cuneus	-6 -84 36
left primary sensory cortex	-48 -18 36
right angular gyrus	54 -48 30
right medial temporal gyrus	52 -43 9

Table 5: MNI coordinates bOS-R task

E Appendix 5

E.1 Between condition analysis comparing action preparation during biologically congruent and incongruent trials in the sOS-R task

The effects of biological congruency in the theta band: The differences between biologically-congruent and biologically-incongruent conditions were examined in the theta band in the sOS-R task but revealed no significant results. The topoplots only showed weak and scattered differences in theta activity throughout the cortex. No clear differences in fronto-central areas could be found and a difference TFR of fronto-central channels did not reveal any differences in the theta band between biologically-congruent and biologically-incongruent conditions during response preparation. Hence, no statistically significant results were found.

The effects of biological congruency in the alpha band: Figure 39A shows the topoplots of the differences in alpha power (9-13 Hz) between biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) in the sOS-R task, which reveal posterior alpha synchronization. A corresponding difference TFR of the affected posterior channels showed that the synchronization started around 500 ms after stimulus movement onset (Figure 39B). As in the sS-R task, the affected alpha band ranged from 9 to 13 Hz. Sensor level statistics comparing the biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) from 0 to 600 ms revealed a significant cluster from 500 ms to 600 ms in posterior channels ($p<0.05$) in accordance with the pattern in the topoplots (Figure 39A). However, no significant differences between biologically-congruent and biologically-incongruent conditions were found in the source level analysis ($p>0.05$).

The effects of biological congruency in the beta band:Figure 39A shows the analysis of the difference between biologically-congruent and biologically-incongruent conditions in the beta (13-25 Hz) band in sOS-R task. The topoplots of the differences between

biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) revealed posterior synchronization and the corresponding difference TFR confirmed that beta activity synchronized from around 500 ms after stimulus movement onset (Figure 39B). Sensor level permutation testing (incongruent-congruent condition) using the time window from 0 to 600 ms and the frequency of 13 to 25 Hz revealed a significant positive cluster in posterior channels between 500 to 600 ms ($p < 0.01$) corresponding to the pattern observed in the topoplots. To localize the beta activity (13-25 hz) a beamformer from 0 to 600 ms did not reveal any significant source level cluster. Based on the TFR of the posterior channels and the sensor level permutation testing it was apparent that the difference between conditions started around 500 ms. A beamformer contrasting the biologically-congruent and biologically-incongruent conditions (incongruent-congruent condition) with the time window 300 to 800 ms localized the positive cluster with global maximum in the left VAA (MNI -30 -78 7) and local maxima in the right VAA (MNI 12 -60 6), left SPL (MNI -30 -54 54) and the left S1 (MNI -36 -36 54, $p<0.05$, Figure 39C). A virtual electrode was placed into the left VAA (global maximum) and plotted as the average beta power per condition over time. This showed that the conditions only differed after 600 ms. For the correlation with the behavioural R-BCy effect statistical testing was applied to the virtual electrode data to select the precise time period during which the two conditions significantly differed. This revealed significant more beta desynchronization in the biologically-congruent in comparison to biologically-incongruent condition between 550 to 620 ms as well as between 650 to 660 ms ($p<0.05$; See, Appendix E Figure 44). However, no significant correlation was found with the behavioural data. Based on these analyses, which show that conditions differ long after stimulus movement onset, it is likely that post-response mechanisms were involved.

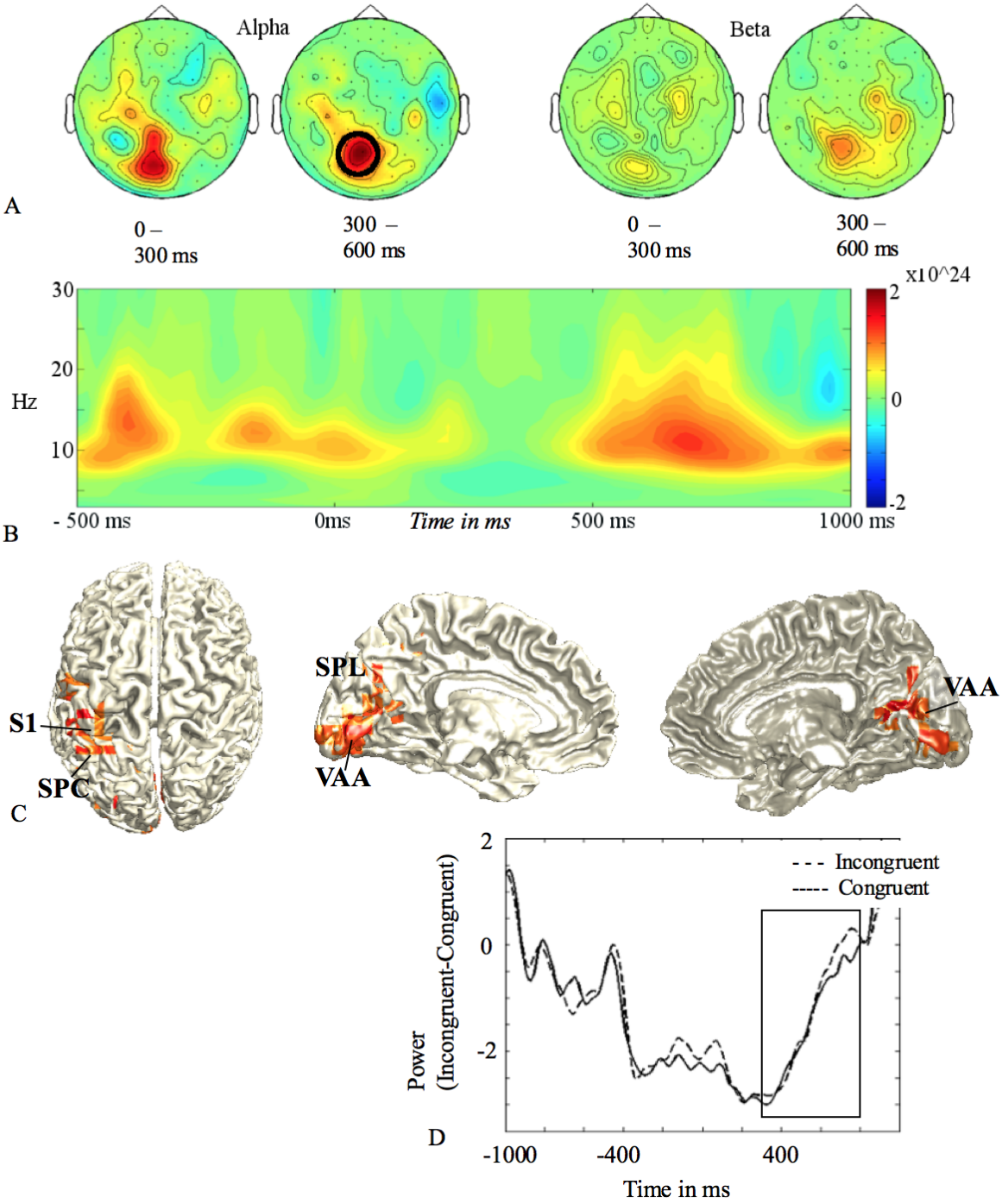


Figure 39: Results from the comparison between biologically-congruent and biologically-incongruent conditions in the alpha and beta bands in the sOS-R task.(A) Topoplots of the differences between conditions (incongruent - congruent condition) of the alpha and beta bands from 0 to 300 ms and from 300 to 600 ms. The black circle indicates the approximate location of the channels used in B. (B) A difference TFR (incongruent-condition condition) from posterior channels with a relative baseline between -1000 to -700 ms. (C) The output of the source localization comparing biologically-congruent and biologically-incongruent conditions (incongruent - congruent conditions) from 300 to 800 ms in the beta band, which shows a significant positive cluster in the bilateral VAA, left SPL and left S1. (D) A virtual electrode located in the global maximum (left VAA) of the cluster in C. The virtual electrode depicts the averaged beta power over time with a relative baseline from -1000 ms to -700 ms. The rectangle corresponds to the time of the beamformer.

E.2 Within condition analysis comparing action preparation during biologically congruent and incongruent trials in the sS-R task.

Theta band changes during rest and action preparation: Figure 40 Panel A shows the time-course of oscillatory theta activity during the sS-R task. In comparison to a relative baseline corresponding to the rest period (-500 to -50 ms), the theta band showed increased frontal synchronization and posterior desynchronization during action preparation (50 to 500 ms). A TFR of left frontal channels showed a synchronization of theta activity from 140 to 600 ms after stimulus movement onset. A beamformer comparing theta activity (4-7 Hz) between action preparation (50 to 600 ms) and rest (-600 to -50 ms) was therefore performed. This revealed a positive cluster with the global maximum in the left M1 (MNI -36 -24 56), left PMC (MNI -44 -8 56) bilateral gyrus rectus (GR; MNI -20 32 -16; 4 56 -16) and right MFG (MNI 44 32 24; $p<0.05$). A virtual electrode was placed into the left M1 and revealed theta synchronization between 200 and 500 ms (Figure 41 Panel A). Simultaneously, a negative cluster was found in more posterior areas ($p<0.001$). This cluster had its global minimum in the left dorsal posterior cingulate cortex (PCC; MNI 12 -80 -8) and a variety of local minima such as the right AG (MNI 28 -80 24), right cerrebellum (MNI 44 -64 -48), right LG (44 -80 -16), right SPL (MNI 44 -80 -16) and left VAA (-12 -80 -8; Figure 41 Panel A). The virtual electrode in the left dorsal PCC showed that the observed negative activity was guided by alpha desynchronization.

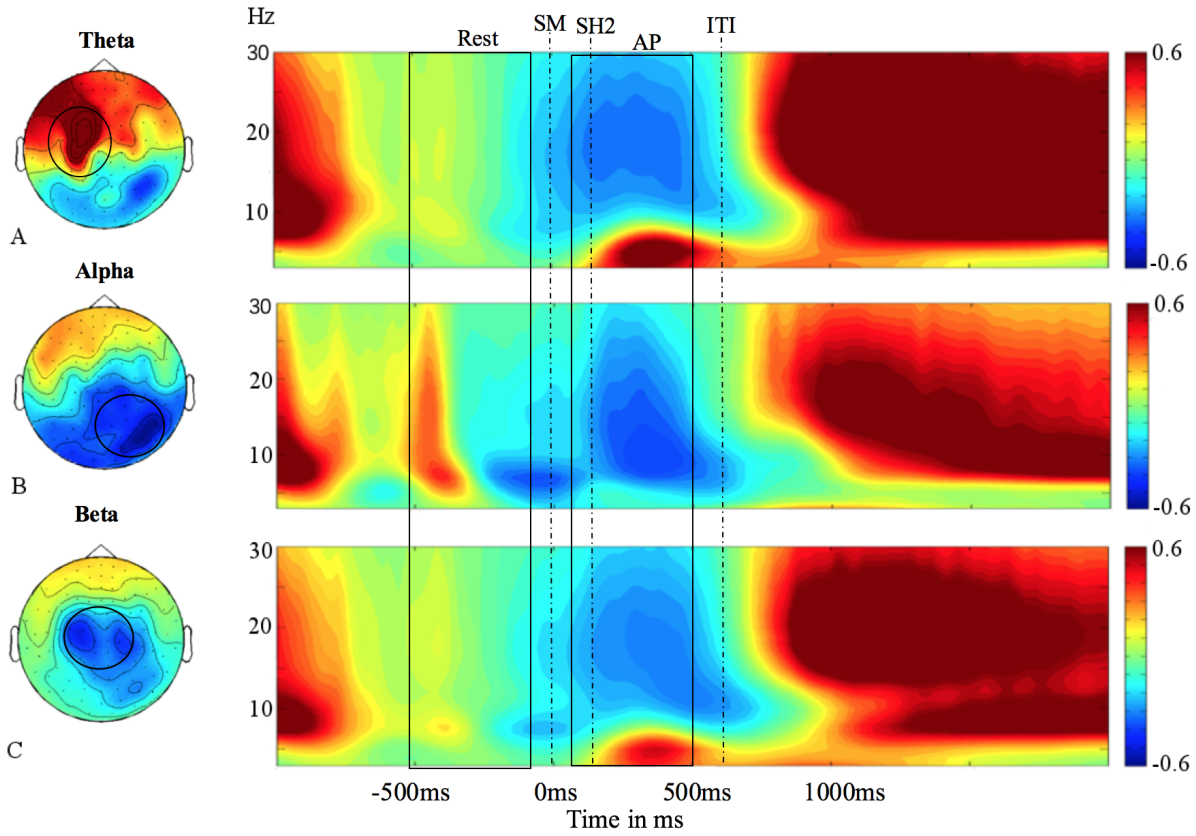


Figure 40: Shows the topoplots of the (A) theta, (B) alpha and (C) beta bands in the sS-R task comparing the rest (-500 to -50 ms) and action preparation (50 to 500 ms) periods (action preparation - rest). A TFR comparing rest and action preparation periods is shown for each frequency band as well. A set of frontal channels was used for the TFR in the theta band (A), a set of posterior channels was used for the TFR in the alpha band (B) and a set of central channels was used for the TFR in the beta band (C). The black circles indicate the approximate location of the chosen channels. All TFRs and topoplots were visualized with a relative baseline corresponding to the rest period (-500 to -50 ms). The solid lines in the TFRs show the rest and action preparation (AP) periods and the dotted lines indicate the onset of the stimulus movement (SM), the second static hand (SH2) and the inter-trials interval (ITI).

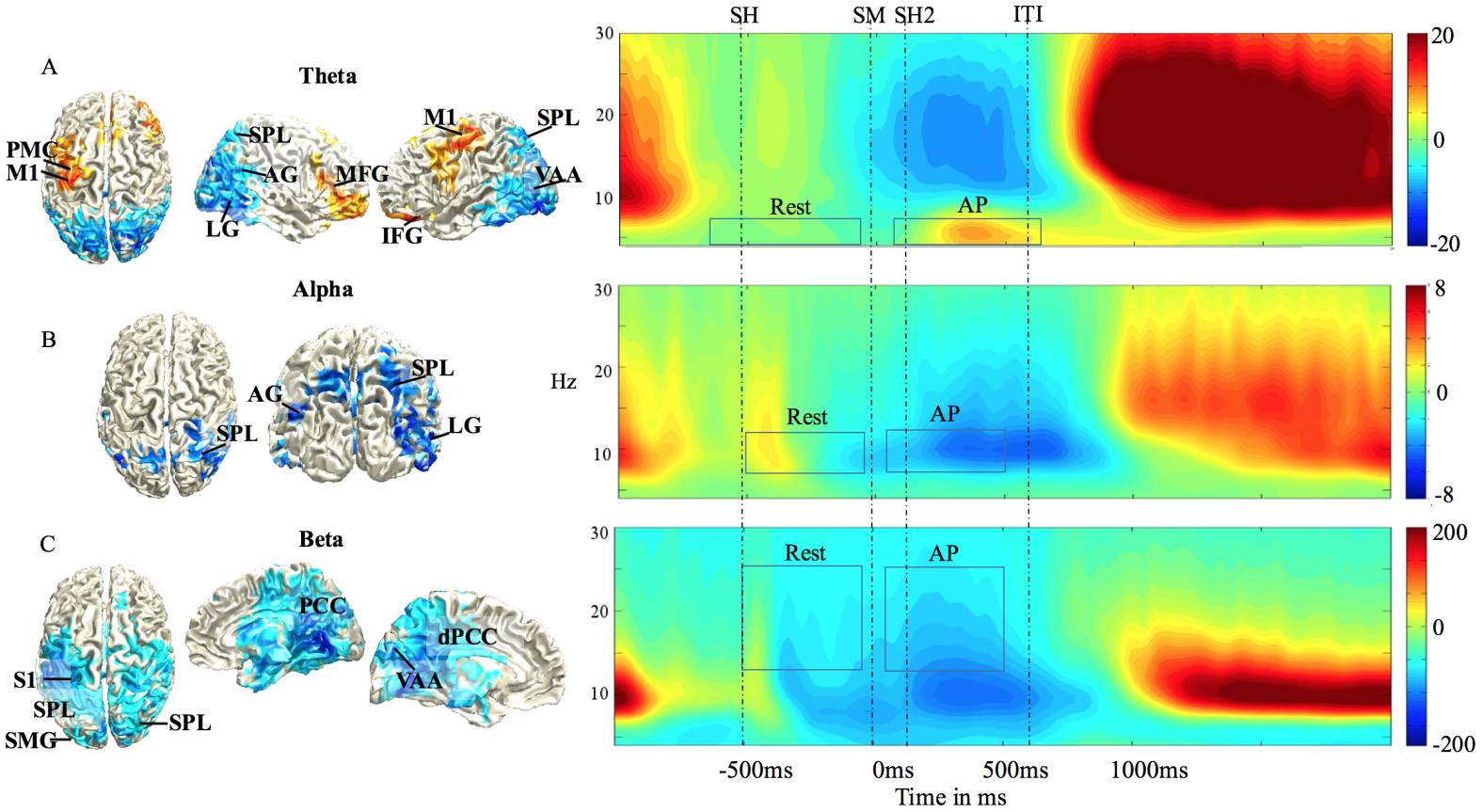


Figure 41: Within-condition source localizations in the sS-R task for (A) theta, (B) alpha and (C) beta bands and the corresponding TFRs of the virtual electrodes placed in the global maximum/minimum of the clusters, which corresponded to the (A) left M1 (B) right cerebellum and (C) right VAA. The source localization in the theta band used a time window from 50 to 600 ms (action preparation, AP) to include more of the theta band observed in the sensor level TFR. The rest period (-600 to 50 ms) was chosen accordingly. For the alpha and beta bands the similar action preparation (50 to 500 ms) and rest (-500 to -50 ms) periods were chosen. The rectangles indicate the rest and action preparation periods (AP) and the dotted lines show the onset of the static hand (SH), the stimulus movement (SM), the second static hand (SH2) and the inter-trial interval (ITI).

Alpha band changes during rest and action preparation: Figure 40 Panel B shows the time-course of oscillatory alpha activity during the sS-R task. In comparison to a relative baseline corresponding to the rest period (-500 to -50 ms), the alpha band showed increased central and posterior desynchronization during action preparation (50 to 500 ms). A TFR with a relative baseline from -500 to -50 ms of the affected posterior channels revealed increased alpha desynchronization throughout the action preparation period (50 to 500 ms). A source localization (8 to 13 Hz) comparing action preparation (50 to 500 ms) to the rest period (-500 to -50 ms; action preparation - rest) revealed a significant negative cluster in the alpha band with global minimum in the right cerebellum (MNI 36 -64 -24) and local minima in the bilateral LG (MNI 52 -73 24, -44 -72 24), bilateral AG (MNI 36 -80 24, -44 -72 32), right SPL (MNI 36 -48 48) and left posterior cingulate gyrus (PCG; -12 -56 16; $p < 0.01$; Figure 41 Panel B). A virtual electrode with a relative baseline was placed into the right cerebellum and confirmed the increased desynchronization during action preparation in comparison to rest (Figure 41 Panel B).

Beta band changes during rest and action preparation:Figure 40 Panel C shows the time-course of oscillatory beta activity during the sS-R task. In comparison to a relative baseline corresponding to the rest period (-500 to -50 ms), the beta band showed increased central desynchronization during action preparation (50 to 500 ms). A TFR of the affected central channels revealed increased beta desynchronization throughout the action preparation period (50 to 500 ms). A source localization (13 to 25 Hz) comparing action preparation (50 to 500 ms) to the rest period (-500 to -50 ms; action preparation - rest) revealed a significant negative cluster with global minimum in the right VAA (MNI 4 -64 8) and local minima in the left VAA (MNI -4 -64 8), right PCC (MNI 4 -56 24), left dorsal PCC (MNI -4 -64 16), left S1 (MNI -44 -21 56) and left AG (MNI -51 -30 38; Figure 41 Panel C). A virtual electrode with a relative baseline was placed in the global minimum of the source level cluster and confirmed the increased desynchronization during action preparation in comparison to rest (Figure 41 Panel C).

E.3 Within condition results comparing rest and action preparation in the sOS-R task

Theta band changes during rest and action preparation: Figure 42 Panel A shows the sensor level plots for the comparison between rest (-500 to -50 ms) and action preparation (50 to 500 ms) in the sOS-R task for the theta band (4 to 7 Hz). The topoplot revealed increased left frontal synchronization and posterior desynchronization during action preparation in comparison to rest using a relative baseline. A corresponding TFR of left frontal channels shows very similar theta synchronization pattern as observed in the sS-R task: synchronization between 200 and 600 ms after stimulus movement onset. Source localization comparing theta activity (4-7 Hz) between action preparation (50 to 600 ms) and rest periods (-600 to -50 ms, action preparation-rest) revealed a borderline significant positive cluster (p=0.059) with global maximum in the left IFG (MNI -36 40 -16) and local minima in the left PO (MNI -60 16 16) and bilateral FPC (MNI -44 40 24, 12 48 -8; Figure 43 Panel A). The virtual electrode with a relative baseline corresponding to the rest period and positioned in the left IFG showed theta synchronization from 200 ms onwards. Further a significant negative cluster with global minimum in the right LG (MNI 28 -80 -16) and local minima in the right VAA (MNI 20 -80 -8), right V1 (MNI 4 -72 16) and right SPL (MNI 12 -64 32) was found (Figure 43 Panel A). As in the sS-R task, the virtual electrode revealed that the negative activity was centred over the alpha band. Hence, the effect in the theta band was likely related to posterior alpha desynchronization.

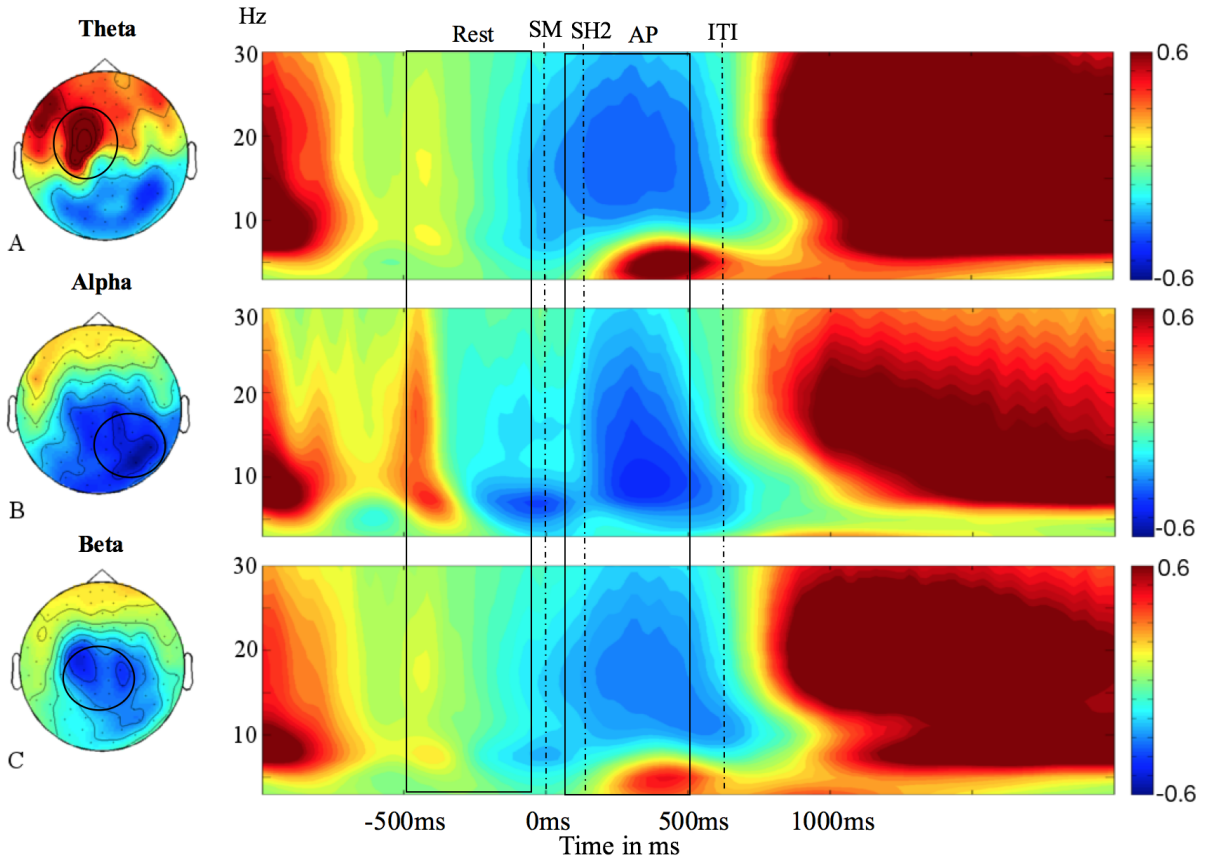


Figure 42: Shows the topoplots of the (A) theta, (B) alpha and (C) beta bands in the sOS-R task comparing the rest (-500 to -50 ms) and action preparation (50 to 500 ms) periods (action preparation - rest). A TFR comparing rest and action preparation periods is shown for each frequency band as well. A set of frontal channels was used for the TFR in the theta band (A), a set of posterior channels was used for the TFR in the alpha band (B) and a set of central channels was used for the TFR in the beta band (C). The black circles indicate the approximate location of the chosen channels. All TFRs and topoplots were visualized with a relative baseline corresponding to the rest period (-500 to -50 ms). The solid lines in the TFRs show the rest and action preparation (AP) periods and the dotted lines indicate the onset of the stimulus movement (SM), the second static hand (SH2) and the inter-trials interval (ITI).

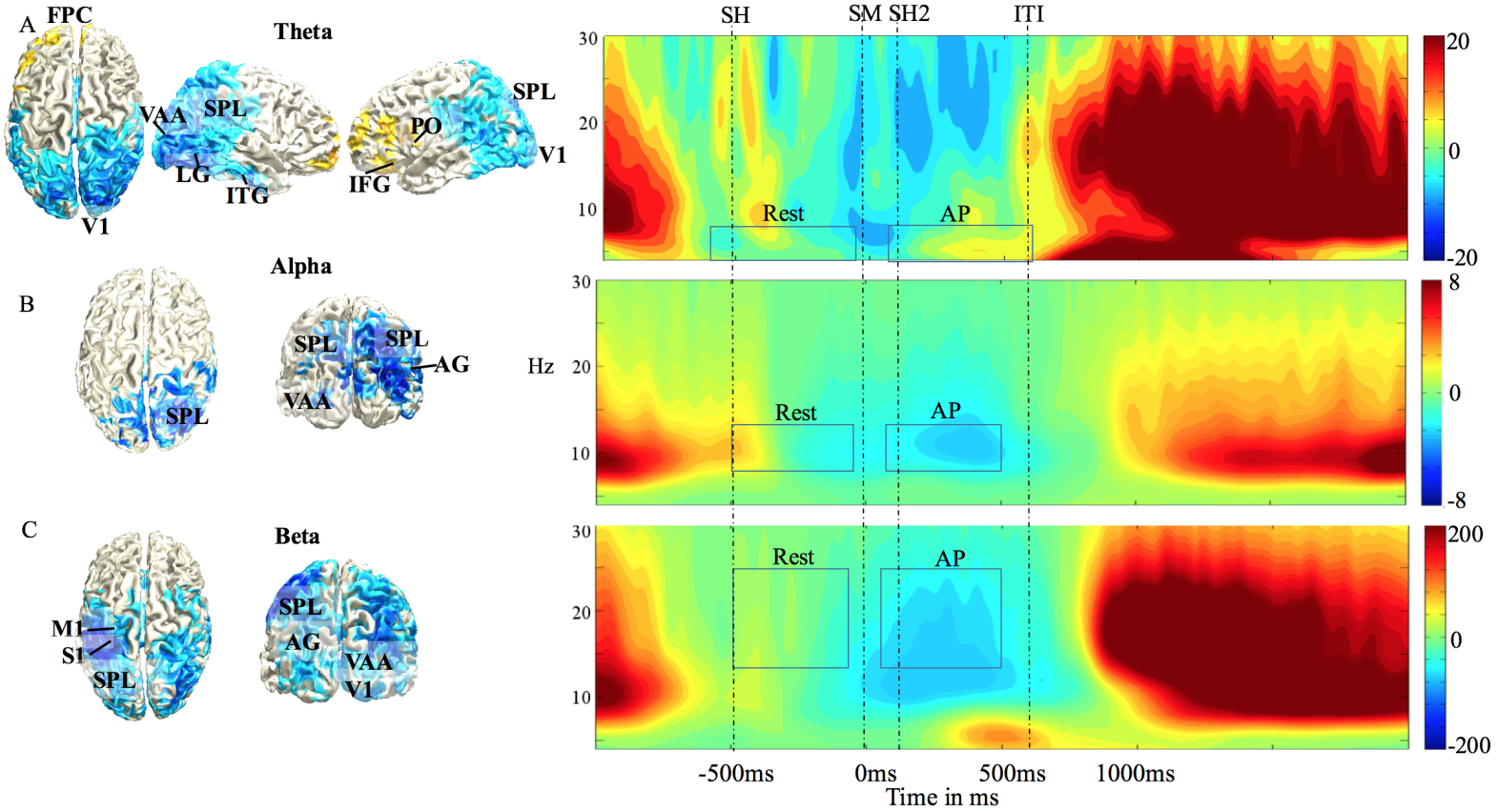


Figure 43: Within-condition source localizations in the sOS-R task for (A) theta, (B) alpha and (C) beta bands and the corresponding TFRs of the virtual electrodes placed in the global maximum/minimum of the clusters, which corresponded to the (A) left IFG, (B) right AG and (C) left S1. The source localization in the theta band used a time window from 50 to 600 ms (action preparation) to include more of the theta synchronization observed in the sensor level TFR. The rest period (-600 to 50 ms) was chosen accordingly. For the alpha and beta bands similar action preparation (50 to 500 ms) and rest (-500 to -50 ms) periods were chosen. The rectangles indicate the rest and action preparation (AP) periods and the dotted lines show the onset of the static hand (SH), the stimulus movement (SM), the second static hand (SH2) and the inter-trial interval (ITI).

Alpha band changes during rest and action preparation: Figure 42 Panel B shows the time-course of oscillatory alpha activity during the sS-R task. In comparison to a relative baseline corresponding to the rest period (-500 to -50 ms), the alpha band showed increased central and posterior desynchronization during action preparation (50 to 500 ms). A TFR of the affected posterior channels revealed increased alpha desynchronization throughout the preparation period (50 to 500 ms). A source localization (8 to 13 Hz) comparing action preparation (50 to 500 ms) to the rest period (-500 to -50 ms; action preparation - rest) revealed a significant negative with the global minimum in the right AG (MNI 36 -85 32) but local minima in the right SPL (MNI 36 -64 56), right LG (36 -88 24) and left VAA (MNI -4 -88 16; $p < 0.05$; Figure 43 Panel B). A virtual electrode was placed in the global minimum of the source level cluster confirmed the increased desynchronization during action preparation in comparison to rest using a relative baseline (Figure 43 Panel B).

Beta band changes during rest and action preparation: Figure 42 Panel C shows the time-course of oscillatory beta activity during the sOS-R task. In comparison to a relative baseline corresponding to the rest period (-500 to -50 ms), the beta band showed increased central desynchronization during action preparation (50 to 500 ms). A corresponding TFR of the affected central channels revealed increased beta desynchronization throughout the preparation period (50 to 500 ms). A source localization (13 to 25 Hz) comparing action preparation (50 to 500 ms) to the rest period (-500 to -50 ms; action preparation - rest) revealed a significant negative cluster with the global minimum in the left S1 (MNI -44 -40 48) and local minima in the left M1 (MNI -19 -27 55), left SPL (MNI -36 -48 64), left AG (MNI -44 -56 56), right VAA (MNI 20 -72 0) and right V1 (MNI 20 -80 8; Figure 43 Panel C). A virtual electrode was placed in the global minimum of the source level cluster and confirmed the increased desynchronization during action preparation in comparison to rest using a relative baseline (Figure 43 Panel C).

E.4 Significant differences between conditions in the virtual electrodes - Experiment 6

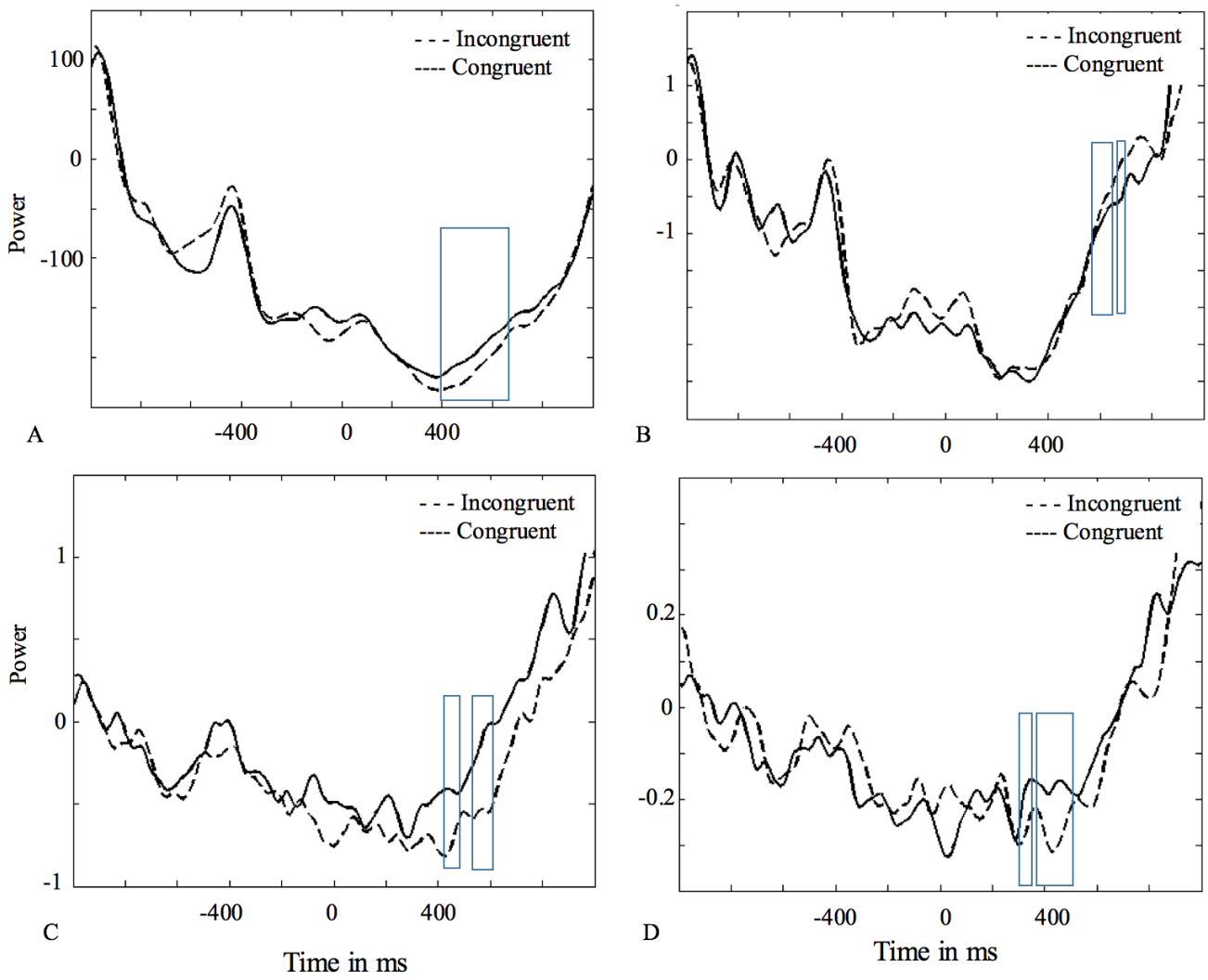


Figure 44: The graphs show the output of the virtual electrode test statistic in the (A,C,D) sS-R and (B) sOS-R tasks of Experiment 6. (A) The virtual electrode positioned in the left LG shows the average alpha power over time in the biologically-congruent and biologically-incongruent conditions (B) The virtual electrode positioned in the left VAA shows the average beta power over time in the biologically-congruent and biologically-incongruent conditions. The virtual electrodes positioned in the left (C) FEF and (D) PO shows the average beta power over time in the biologically-congruent and biologically-incongruent conditions. The rectangles indicate the periods where the conditions significantly differed.

E.5 MNI coordinates - Experiment 6

sS-R Theta	MNI
left primary motor cortex	-36 -24 56
left premotor cortex	-44 -8 56
bilateral gyrus rectus	-20 32 -16; 4 56 -16
right middle frontal gyrus	44 32 24
left dorsal posterior cingulate cortex	12 -80 -8
right angular gyrus	28 -80 24
right cerrebellum	44 -64 -48
right lingual gyrus	44 -80 -16
right superior parietal lobule	44 -80 -16
left visual association area	-12 -80 -8
left somatosensory cortex	-30 -35 48
left primary motor cortex	-30 -24 68
sS-R Alpha	MNI
right cerebellum	36 -64 -24
bilateral lingual gyrus	52 -73 24, -44 -72 24
bilateral angular gyrus	36 -80 24, -44 -72 32
right superior parietal cortex	36 -48 48
left posterior cingulate gyrus	-12 -56 16
right primary visual cortex	6 -84 0
left lingual gyrus	-12 -48 0
left angular gyrus	-30 -60 30
sS-R Beta	MNI
the right visual association area	4 -64 8
left visual association cortex	-4 -64 8
heightright posterior cingulate cortex	4 -56 24
left dorsal posterior cingulate cortex	-4 -64 16
left primary sensory area	-44 -21 56
left supramaginal gyrus	-51 -30 38
left medial frontal gyrus	-32 14 44
the frontal eye fields	-36 24 42
left pars opercularis	-60 12 12
supramarginal gyrus	-54 -30 30

Table 6: MNI coordinates sS-R task

sOS-R Theta	MNI
left inferior frontal gyrus	-36 40 -16
left pars opercularis	-60 16 16
bilateral frontopolar cortex	-44 40 24, 12 48 -8
right lingual gyrus	28 -80 -16
the right visual association cortex	20 -80 -8
right primary visual cortex	4 -72 16
right superior parietal cortex	12 -64 32
sOS-R Alpha	MNI
right angular gyrus	36 -85 32
right superior parietal lobule	36 -64 56
right lingual gyrus	36 -88 24
left visual association area	-4 -88 16
sOS-R Beta	MNI
left primary sensory area	-44 -40 48
left primary motor cortex	-19 -27 55
left superior parietal lobule	-36 -48 64
left angular gyrus	-44 -56 56
right visual association area	20 -72 0
right primary visual cortex	20 -80 8
left visual association area	-30 -78 7
right visual association area	12 -60 6
left superior parietal lobule	-30 -54 54
left primary sensory cortex	-36 -36 54

Table 7: MNI coordinates sOS-R task

References

Ali, N., Green, D. W., Kherif, F., Devlin, J. T., & Price, C. J. (2010). The Role of the Left Head of Caudate in Suppressing Irrelevant Words. *Journal of Cognitive Neuroscience*, *22*(10), 2369–2386. doi: 10.1162/jocn.2009.21352

Amoruso, L., & Urgesi, C. (2016). Contextual modulation of motor resonance during the observation of everyday actions. *NeuroImage*, *134*, 74–84. doi: 10.1016/j.neuroimage.2016.03.060

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual review of neuroscience*, *20*(1), 303–330.

Ansorge, U. (2003). *Spatial Simon effects and compatibility effects induced by observed gaze direction* (Vol. 10) (No. 3). doi: 10.1080/13506280244000122

Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011). -Suppression during Action Observation and Execution Correlates with BOLD in Dorsal Premotor, Inferior Parietal, and SI Cortices. *Journal of Neuroscience*, *31*(40), 14243–14249. doi: 10.1523/JNEUROSCI.0963-11.2011

Aschersleben, G., & Prinz, W. (1995). Synchronizing actions with events: The role of sensory information. *Perception & Psychophysics*, *57*(3), 305–317.

Avenanti, A., Bolognini, N., Maravita, A., & Aglioti, S. M. (2007). Somatic and motor components of action simulation. *Current Biology*, *17*(24), 2129–2135.

Avikainen, S., Wohlschläger, A., Liuhanen, S., Hänninen, R., & Hari, R. (2003). Impaired mirror-image imitation in asperger and high-functioning autistic subjects. *Current biology*, *13*(4), 339–341.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., ... Rossini, P. M. (2002). Human cortical electroencephalography (eeg) rhythms during the observation of simple aimless movements: a high-resolution eeg study. *Neuroimage*, *17*(2), 559–572.

Balleine, B. W., & Dickinson, A. (1998). Goal-directed instrumental action: Contingency

and incentive learning and their cortical substrates. *Neuropharmacology*, *37*(4-5), 407–419. doi: 10.1016/S0028-3908(98)00033-1

Bandura, A. (1962). Social learning through imitation.

Barber, P., & O'Leary, M. (1997). The relevance of salience: Towards an activational account of irrelevant stimulus-response compatibility effects. In *Advances in psychology* (Vol. 118, pp. 135–172). Elsevier.

Barchiesi, G., & Cattaneo, L. (2012). Early and late motor responses to action observation. *Social cognitive and affective neuroscience*, *8*(6), 711–719.

Bardi, L., Kanai, R., Mapelli, D., & Walsh, V. (2012). Tms of the fef interferes with spatial conflict. *Journal of cognitive neuroscience*, *24*(6), 1305–1313.

Bernier, R., Aaronson, B., & McPartland, J. (2013). The role of imitation in the observed heterogeneity in EEG mu rhythm in autism and typical development. *Brain and Cognition*, *82*(1), 69–75. doi: 10.1016/j.bandc.2013.02.008

Bernier, R., Dawson, G., Webb, S., & Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain and Cognition*, *64*(3), 228–237. doi: 10.1016/j.bandc.2007.03.004

Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative Response Tendencies Following Observation of Intransitive Actions. , *32*(2), 210–225. doi: 10.1037/0096-1523.32.2.210

Bien, N., Roebroeck, A., Goebel, R., & Sack, A. T. (2009). The Brain's intention to imitate: The neurobiology of intentional versus automatic imitation. *Cerebral Cortex*, *19*(10), 2338–2351. doi: 10.1093/cercor/bhn251

Biermann-Ruben, K., Kessler, K., Jonas, M., Siebner, H. R., Bäumer, T., Münchau, A., & Schnitzler, A. (2008). Right hemisphere contributions to imitation tasks. *European Journal of Neuroscience*, *27*(7), 1843–1855. doi: 10.1111/j.1460-9568.2008.06146.x

Bock. (1986). Syntactic Persistence in Language Production. , *387*, 355–387.

Borich, M. R., Brodie, S. M., Gray, W. A., Ionta, S., & Boyd, L. A. (2016). Understanding the role of the primary somatosensory cortex: Opportunities for rehabil-

itation. *Neuropsychologia*, *79*, 246–255. doi: 10.1016/j.neuropsychologia.2015.07.007.Understanding

Bornstein, R. F., Leone, D. R., & Galley, D. J. (1987). The generalizability of subliminal mere exposure effects: Influence of stimuli perceived without awareness on social behavior. *Journal of personality and social psychology*, *53*(6), 1070.

Boyer, T. W., Longo, M. R., & Bertenthal, B. I. (2012). Is automatic imitation a specialized form of stimulus–response compatibility? dissociating imitative and spatial compatibilities. *Acta Psychologica*, *139*(3), 440–448.

Boyer, T. W., Scheutz, M., & Bertenthal, B. I. (2009). Dissociating ideomotor and spatial compatibility: Empirical evidence and connectionist models. In *Proceedings of the 31st annual conference of the cognitive science society* (pp. 2280–2285).

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*(1-2), 3–22. doi: 10.1016/S0001-6918(00)00024-X

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*(2), 124–143. doi: 10.1006/brcg.2000.1225

Brass, M., Derrfuss, J., & Von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: A functional double dissociation. *Neuropsychologia*, *43*(1), 89–98. doi: 10.1016/j.neuropsychologia.2004.06.018

Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *Journal of Neuroscience*, *28*(40), 10056–10061.

Brittain, J.-S., Watkins, K. E., Joundi, R. A., Ray, N. J., Holland, P., Green, A. L., ... Jenkinson, N. (2012). A Role for the Subthalamic Nucleus in Response Inhibition during Conflict. *Journal of Neuroscience*, *32*(39), 13396–13401. doi: 10.1523/JNEUROSCI.2259-12.2012

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G.

(2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, *42*(2), 323–334. doi: 10.1016/S0896-6273(04)00181-3

Bush, G., Shin, L. M., Holmes, J., Rosen, B. R., & Vogt, B. A. (2003). The multi-source interference task: Validation study with fMRI in individual subjects. *Molecular Psychiatry*, *8*(1), 60–70. doi: 10.1038/sj.mp.4001217

Caggiano, V., Fogassi, L., Rizzolatti, G., Casile, a., Giese, M. a., & Thier, P. (2012). Mirror neurons encode the subjective value of an observed action. *Proceedings of the National Academy of Sciences*, *109*(29), 11848–11853. doi: 10.1073/pnas.1205553109

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., & Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *science*, *324*(5925), 403–406.

Cao, Y., Cao, X., Yue, Z., & Wang, L. (2017). Temporal and spectral dynamics underlying cognitive control modulated by task-irrelevant stimulus-response learning. *Cognitive, Affective and Behavioral Neuroscience*, *17*(1), 158–173. doi: 10.3758/s13415-016-0469-5

Carlqvist, H., Nikulin, V. V., Strömberg, J.-O., & Brismar, T. (2005). Amplitude and phase relationship between alpha and beta oscillations in the human electroencephalogram. *Medical and Biological Engineering and Computing*, *43*(5), 599–607.

Carpenter, M., Uebel, J., & Tomasello, M. (2013). Being mimicked increases prosocial behavior in 18-month-old infants. *Child development*, *84*(5), 1511–1518.

Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008). Through the looking glass: Counter-mirror activation following incompatible sensorimotor learning. *European Journal of Neuroscience*, *28*(6), 1208–1215.

Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and spatial compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(2), 409.

Catmur, C., & Heyes, C. (2013). Is it what you do, or when you do it? the roles of contingency and similarity in pro-social effects of imitation. *Cognitive science*,

37(8), 1541–1552.

Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. (2011). Making mirrors: premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of cognitive neuroscience*, *23*(9), 2352–2362. doi: 10.1162/jocn.2010.21590

Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor Learning Configures the Human Mirror System. *Current Biology*, *17*(17), 1527–1531. doi: 10.1016/j.cub .2007.08.006

Catmur, C., Walsh, V., & Heyes, C. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2369–2380. doi: 10.1098/rstb.2009.0048

Cattaneo, L. (2010). Tuning of ventral premotor cortex neurons to distinct observed grasp types: a tms-priming study. *Experimental brain research*, *207*(3-4), 165–172.

Cattaneo, L., Barchiesi, G., Tabarelli, D., Arfeller, C., Sato, M., & Glenberg, A. M. (2010). One's motor performance predictably modulates the understanding of others' actions through adaptation of premotor visuo-motor neurons. *Social Cognitive and Affective Neuroscience*, *6*(3), 301–310.

Cavallo, A., Heyes, C., Becchio, C., Bird, G., & Catmur, C. (2013). Timecourse of mirror and counter-mirror effects measured with transcranial magnetic stimulation. *Social cognitive and affective neuroscience*, *9*(8), 1082–1088.

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: Eeg phase synchrony reveals cognitive control dynamics during action monitoring. *Journal of Neuroscience*, *29*(1), 98–105.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, *18*(8), 414–421. doi: 10.1016/j.tics.2014.04.012

Cavanagh, J. F., Frank, M. J., Klein, T. J., & Allen, J. J. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *Neuroimage*, *49*(4), 3198–3209.

Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology*, *49*(2), 220–238. doi: 10.1111/j.1469-8986.2011.01293.x

Charness, G., Gneezy, U., & Kuhn, M. A. (2012). Journal of Economic Behavior & Organization Experimental methods : Between-subject and within-subject design. *Journal of Economic Behavior and Organization*, *81*(1), 1–8. Retrieved from `http://dx.doi.org/10.1016/j.jebo.2011.08.009` doi: 10.1016/j.jebo.2011.08.009

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception–behavior link and social interaction. *Journal of personality and social psychology*, *76*(6), 893.

Chartrand, T. L., & Lakin, J. L. (2013). The antecedents and consequences of human behavioral mimicry. *Annual review of psychology*, *64*, 285–308.

Chartrand, T. L., & Van Baaren, R. (2009). Human mimicry. *Advances in experimental social psychology*, *41*, 219–274.

Chatrian, G. E., Petersen, M. C., & Lazarte, J. A. (1959). The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroencephalography and clinical neurophysiology*, *11*(3), 497–510.

Cheyne, D. O. (2013). Meg studies of sensorimotor rhythms: a review. *Experimental neurology*, *245*, 27–39.

Chiavarino, C., Apperly, I. A., & Humphreys, G. W. (2007). Exploring the functional and anatomical bases of mirror-image and anatomical imitation: the role of the frontal lobes. *Neuropsychologia*, *45*(4), 784–795.

Cisek, P., & Kalaska, J. F. (2004). Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature*, *431*(7011), 993–996. doi: 10.1038/nature03005

Cohen, M. X. (2011). Error-related medial frontal theta activity predicts cingulate-related structural connectivity. *NeuroImage*, *55*(3), 1373–1383. doi: 10.1016/j.neuroimage.2010.12.072

Cohen, M. X., Bour, L., Mantione, M., Figee, M., Vink, M., Tijssen, M. A., ... Denys, D. (2012). Top–down-directed synchrony from medial frontal cortex to nucleus

accumbens during reward anticipation. *Human brain mapping*, *33*(1), 246–252.

Cohen, M. X., & Cavanagh, J. F. (2011). Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. *Frontiers in psychology*, *2*, 30.

Cohen, M. X., & Ridderinkhof, K. R. (2013). EEG Source Reconstruction Reveals Frontal-Parietal Dynamics of Spatial Conflict Processing. *PLoS ONE*, *8*(2). doi: 10.1371/journal.pone.0057293

Cohen, M. X., Ridderinkhof, K. R., Haupt, S., Elger, C. E., & Fell, J. (2008). Medial frontal cortex and response conflict: Evidence from human intracranial EEG and medial frontal cortex lesion. *Brain Research*, *1238*, 127–142. doi: 10.1016/j.brainres .2008.07.114

Cohen, M. X., Van Gaal, S., Ridderinkhof, K. R., & Lamme, V. (2009). Unconscious errors enhance prefrontal-occipital oscillatory synchrony. *Frontiers in human neuroscience*, *3*, 54.

Coll, M.-P., Bird, G., Catmur, C., & Press, C. (2015). Cross-modal repetition effects in the mu rhythm indicate tactile mirroring during action observation. *Cortex*, *63*, 121–131.

Coll, M.-P., Press, C., Hobson, H., Catmur, C., & Bird, G. (2017). Crossmodal classification of mu rhythm activity during action observation and execution suggests specificity to somatosensory features of actions. *Journal of Neuroscience*, *37*(24), 5936–5947.

Compton, R. J., Arnstein, D., Freedman, G., Dainer-Best, J., & Liss, A. (2011). Cognitive control in the intertrial interval: Evidence from EEG alpha power. *Psychophysiology*, *48*(5), 583–590. doi: 10.1111/j.1469-8986.2010.01124.x

Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: From origin to function. *Behavioral and Brain Sciences*, *37*(2), 177–192. doi: 10.1017/S0140525X13000903

Cooper, R. P., Catmur, C., & Heyes, C. (2013). Are automatic imitation and spatial compatibility mediated by different processes? *Cognitive Science*, *37*(4), 605–630.

doi: 10.1111/j.1551-6709.2012.01252.x

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. doi: 10.1038/nrn755

Craft, J. L., & Simon, J. R. (1970). Processing symbolic information from a visual display: Interference from an irrelevant directional cue. *Journal of Experimental Psychology*, *83*(3 PART 1), 415–420. doi: 10.1037/h0028843

Cross, K. A., Torrisi, S., Reynolds Losin, E. A., & Iacoboni, M. (2013). Controlling automatic imitative tendencies: Interactions between mirror neuron and cognitive control systems. *NeuroImage*, *83*, 493–504. doi: 10.1016/j.neuroimage.2013.06.060

Dassonville, P., Lewis, S. M., Zhu, X. H., Ugurbil, K., Kim, S. G., & Ashe, J. (2001). The effect of stimulus-response compatibility on cortical motor activation. *NeuroImage*, *13*(1), 1–14. doi: 10.1006/nimg.2000.0671

De Jong, R., Liang, C.-C., & Lauber, E. (1994). Conditional and unconditional automaticity: a dual-process model of effects of spatial stimulus-response correspondence. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(4), 731.

Désy, M. C., & Lepage, J. F. (2013). Skin color has no impact on motor resonance: Evidence from mu rhythm suppression and imitation. *Neuroscience Research*, *77*(1-2), 58–63. doi: 10.1016/j.neures.2013.08.003

Dinstein, I., Hasson, U., Rubin, N., & Heeger, D. J. (2007). Brain Areas Selective for Both Observed and Executed Movements. *Journal of Neurophysiology*, *98*(3), 1415–1427. doi: 10.1152/jn.00238.2007

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research*, *91*(1), 176–180.

Eimer, M. (1995). Stimulus-Response Compatibility and Automatic Response Activation: Evidence From Psychophysiological Studies. *Journal of Experimental Psychology:*

Human Perception and Performance, *21*(4), 837–854. doi: 10.1037/0096-1523.21.4.837

Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(1), 229–240. doi: 10.1037/0096-1523.27.1.229

Elsner, B., Hommel, B., Mentschel, C., Drzezga, A., Prinz, W., Conrad, B., & Siebner, H. (2002). Linking actions and their perceivable consequences in the human brain. *NeuroImage*, *17*(1), 364–372. doi: 10.1006/nimg.2002.1162

Engel, A., Burke, M., Fiehler, K., Bien, S., & Rösler, F. (2008). How moving objects become animated: the human mirror neuron system assimilates non-biological movement patterns. *Social neuroscience*, *3*(3-4), 368–387.

Enticott, P. G., Rinehart, N. J., Tonge, B. J., Bradshaw, J. L., & Fitzgerald, P. B. (2010). A preliminary transcranial magnetic stimulation study of cortical inhibition and excitability in high-functioning autism and Asperger disorder. *Developmental Medicine & Child Neurology*, *52*(8), e179-e183. doi: 10.1111/j.1469-8749.2010.03665.x

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Physiology*, *73*(6), 2608–2611.

Fan, J., Flombaum, J. I., McCandliss, B. D., Thomas, K. M., & Posner, M. I. (2003). Cognitive and brain consequences of conflict. *NeuroImage*, *18*(1), 42–57. doi: 10.1006/nimg.2002.1319

Fan, Y.-t., Decety, J., Yang, C.-y., Liu, J.-l., & Cheng, Y. (2010). Unbroken mirror neurons in autism spectrum disorders. *Journal of Child Psychology and Psychiatry*, *51*(9), 981–988. doi: 10.1111/j.1469-7610.2010.02269.x

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience*, *17*(8), 1703–1714. doi:

10.1046/j.1460-9568.2003.02601.x

Fogassi, L., Ferrari, P., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal Lobe: From Action Organization to Intention Understanding. *Science*, *308*(2005), 662–667. doi: 10.1126/science.1106138

Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the n2 component of the erp: a review. *Psychophysiology*, *45*(1), 152–170.

Fox, N. A., Yoo, K. H., Bowman, L. C., Cannon, E. N., Ferrari, P. F., Bakermans-Kranenburg, M. J., ... Van IJzendoorn, M. H. (2016). Assessing human mirror activity With EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, *142*(3), 291–313. doi: 10.1037/bul0000031

Galashan, D., Wittfoth, M., Fehr, T., & Herrmann, M. (2008). Two Simon tasks with different sources of conflict: An ERP study of motion- and location-based compatibility effects. *Biological Psychology*, *78*(3), 246–252. doi: 10.1016/j.biopsycho.2008.03.008

Gallese, V. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593–609.

Galletti, C., Breveglieri, R., Lappe, M., Bosco, A., Ciavarro, M., & Fattori, P. (2010). Covert shift of attention modulates the ongoing neural activity in a reaching area of the macaque dorsomedial visual stream. *PLoS ONE*, *5*(11). doi: 10.1371/journal.pone.0015078

Gastaut, H. J., & Bert, J. (1954). Eeg changes during cinematographic presentation (moving picture activation of the eeg). *Electroencephalography and clinical neurophysiology*, *6*, 433–444.

Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*(4), 1674–1684. doi: 10.1016/j.neuroimage.2007.02.003

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*(4), 374–385. doi: 10.1093/cercor/

7.4.374

Gilbertson, T. (2005). Existing Motor State Is Favored at the Expense of New Movement during 13-35 Hz Oscillatory Synchrony in the Human Corticospinal System. *Journal of Neuroscience*, *25*(34), 7771–7779. doi: 10.1523/JNEUROSCI.1762-05.2005

Gleissner, B., Bekkering, H., & Meltzoff, A. N. (2000). Children's coding of human action: cognitive factors influencing imitaation in 3-year-old. *Developmental Science*, *3*(4), 405–414.

Gola, M., Magnuski, M., Szumska, I., & Wróbel, A. (2013). EEG beta band activity is related to attention and attentional deficits in the visual performance of elderly subjects. *International Journal of Psychophysiology*, *89*(3), 334–341. doi: 10.1016/j.ijpsycho.2013.05.007

Goldenberg, G., & Karnath, H.-O. (2006). The neural basis of imitation is body part specific. *Journal of Neuroscience*, *26*(23), 6282–6287.

Gottlieb, J. (2007). From thought to action: the parietal cortex as a bridge between perception, action, and cognition. *Neuron*, *53*(1), 9–16.

Gowen, E., Bradshaw, C., Galpin, A., Lawrence, A., & Poliakoff, E. (2010). Exploring visuomotor priming following biological and non-biological stimuli. *Brain and Cognition*, *74*(3), 288–297. doi: 10.1016/j.bandc.2010.08.010

Grahn, J. A., Parkinson, J. A., & Owen, A. M. (2008). The cognitive functions of the caudate nucleus. *Progress in Neurobiology*, *86*(3), 141–155. Retrieved from `http://linkinghub.elsevier.com/retrieve/pii/S0301008208001019` doi: 10.1016/j.pneurobio.2008.09.004

Green, J. J., & McDonald, J. J. (2008). Electrical neuroimaging reveals timing of attentional control activity in human brain. *PLoS Biology*, *6*(4), 730–738. doi: 10.1371/journal.pbio.0060081

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. (2001). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences*, *98*(2), 694–699.

doi: 10.1073/pnas.98.2.694

Guéguen, N., Martin, A., & Meineri, S. (2011). Mimicry and helping behavior: An evaluation of mimicry on explicit helping request. *The Journal of social psychology*, *151*(1), 1–4.

Händel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha Oscillations Correlate with the Successful Inhibition of Unattended Stimuli. , 2494–2502.

Hanslmayr, S., Pastötter, B., Bäuml, K. H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the stroop task. *Journal of Cognitive Neuroscience*, *20*(2), 215–225. doi: 10.1162/jocn.2008.20020

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences*, *95*(25), 15061–15065.

Hari, R., Levänen, S., & Raij, T. (2000). Timing of human cortical functions during cognition: Role of MEG. *Trends in Cognitive Sciences*, *4*(12), 455–462. doi: 10 .1016/S1364-6613(00)01549-7

Harper, J., Malone, S. M., & Bernat, E. M. (2014). Theta and delta band activity explain n2 and p3 erp component activity in a go/no-go task. *Clinical Neurophysiology*, *125*(1), 124–132.

Hasbroucq, T., & Guiard, Y. (1991). Stimulus-response compatibility and the Simon effect: toward a conceptual clarification. *Journal of experimental psychology. Human perception and performance*, *17*(1), 246–266. doi: 10.1037/0096-1523.17.1.246

Hedge, A., & Marsh, N. (1975). The effect of irrelevant spatial correspondences on two-choice response-time. *Acta psychologica*, *39*(6), 427–439.

Heister, G., Ehrenstein, W. H., & Schroeder-Heister, P. (1987). Spatial sr compatibility with unimanual two-finger choice reactions: Effects of irrelevant stimulus location. *Perception & Psychophysics*, *42*(2), 195–201.

Heyes, C. (2011). Automatic Imitation. *Psychological Bulletin*, *137*(3), 463–483. doi: 10.1037/a0022288

Hobson, H. M., & Bishop, D. V. (2016). Mu suppression – A good measure of the human mirror neuron system? *Cortex*, *82*, 290–310. doi: 10.1016/j.cortex.2016.03.019

Hobson, H. M., & Bishop, D. V. (2017). The interpretation of mu suppression as an index of mirror neuron activity: past, present and future. *Royal Society open science*, *4*(3), 160662.

Hommel, B. (1993). The role of attention for the Simon effect. *Psychological Research*, *55*(3), 208–222. doi: 10.1007/BF00419608

Hommel, B. (2011). The Simon effect as tool and heuristic. *Acta Psychologica*, *136*(2), 189–202. doi: 10.1016/j.actpsy.2010.04.011

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current opinion in neurobiology*, *15*(6), 632–637.

Itthipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Experimental brain research*, *224*(2), 255–262.

Jacobson, S. W. (1979). Matching Behavior in the Young Infant. *Child Development*, *50*(2), 425–430.

Jacquet, P. O., & Avenanti, A. (2013). Perturbing the action observation network during perception and categorization of actions' goals and grips: state-dependency and virtual lesion tms effects. *Cerebral Cortex*, *25*(3), 598–608.

James, W. (1890). *The principles of psychology*. New York: Dover Publications.

Jansson, E., Wilson, A. D., Williams, J. H., & Mon-Williams, M. (2007). Methodological problems undermine tests of the ideo-motor conjecture. *Experimental Brain Research*, *182*(4), 549–558. doi: 10.1007/s00221-007-1013-1

Jenkinson, N., & Brown, P. (2011). New insights into the relationship between dopamine, beta oscillations and motor function. *Trends in neurosciences*, *34*(12), 611–618.

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *Neuroscience*, *15*(8), 1395–1399. doi: 10.1046/j.1460-9568.2002.01975.x

Jonas, M., Biermann-Ruben, K., Kessler, K., Lange, R., Bäumer, T., Siebner, H., ... Münchau, A. (2007). Observation of a finger or an object movement primes imitative responses differentially. *Experimental Brain Research*, *177*(2), 255–265.

Jones, S. S. (2006). Exploration or imitation? The effect of music on 4-week-old infants' tongue protrusions. *Infant Behavior and Development*, *29*(1), 126–130. doi: 10 .1016/j.infbeh.2005.08.004

Kerns, J. G. (2006). Anterior cingulate and prefrontal cortex activity in an fmri study of trial-to-trial adjustments on the simon task. *Neuroimage*, *33*(1), 399–405.

Kessler, K., Biermann-Ruben, K., Jonas, M., Roman Siebner, H., Bäumer, T., Münchau, A., & Schnitzler, A. (2006). Investigating the human mirror neuron system by means of cortical synchronization during the imitation of biological movements. *NeuroImage*, *33*(1), 227–238. doi: 10.1016/j.neuroimage.2006.06.014

Keuken, M. C., Hardie, A., Dorn, B., Dev, S., Paulus, M., Jonas, K., ... Pineda, J. (2011). The role of the left inferior frontal gyrus in social perception: an rtms study. *Brain research*, *1383*, 196–205.

Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups and downs of beta oscillations in sensorimotor cortex. *Experimental neurology*, *245*, 15–26.

Kilner, J. M., Baker, S. N., Salenius, S., Jousm, V., Hari, R., & Lemon, R. N. (1999). Task-dependent modulation of 15-30 Hz coherence between rectified EMGs from human hand and forearm muscles. *Journal of Physiology*, *516*(2), 559–570. doi: 10.1111/j.1469-7793.1999.0559v.x

Kilner, J. M., & Lemon, R. N. (2013). What we know currently about mirror neurons. *Current biology*, *23*(23), R1057–R1062.

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience*, *29*(32), 10153–10159. doi: 10.1523/JNEUROSCI.2668-09.2009

Kilner, J. M., Paulignan, Y., & Blakemore, S.-J. (2003). An interference effect of observed

biological movement on action. *Current biology*, *13*(6), 522–525.

Klimesch, & W. (1997). Alpha rhythms and memory processes. *International Journal of Psychophysiology*, *26*, 319–340.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain research.Brain research reviews*, *29*(2-3), 169–195.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in cognitive sciences*, *16*(12), 606–617.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. doi: 10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schimke, H., & Pfurtscheller, G. (1993). Alpha frequency, cognitive load and memory performance. *Brain topography*, *5*(3), 241–251.

Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., & Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage*, *40*(2), 767–775. doi: 10.1016/j.neuroimage.2007.12.018

Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitve basis for stimulus-response compatibility – a model and taxonomy. *Psychological Review*, *97*(2), 253–270.

Koski, L., Iacoboni, M., Dubeau, M.-C., Woods, R. P., & Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of neurophysiology*, *89*(1), 460–471.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological science*, *14*(4), 334–339.

Lange, J., Pavlidou, A., & Schnitzler, A. (2015). Lateralized modulation of beta-band power in sensorimotor areas during action observation. *Frontiers in Integrative Neuroscience*, *9*(June), 1–8.

Lansing, R. W., Schwartz, E., & Lindsley, D. B. (1959). Reaction time and eeg activation

under alerted and nonalerted conditions. *Journal of experimental psychology*, *58*(1), 1.

Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *NeuroImage*, *19*(4), 1463–1476. doi: 10.1016/S1053-8119(03)00286-6

Leighton, J., Bird, G., Orsini, C., & Heyes, C. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology*, *46*(6), 905–910.

Leuthold, H. (2011). The Simon effect in cognitive electrophysiology: A short review. *Acta Psychologica*, *136*(2), 203–211. Retrieved from `http://dx.doi.org/10.1016/j.actpsy.2010.08.001` doi: 10.1016/j.actpsy.2010.08.001

Li, C.-s. R., Yan, P., Sinha, R., & Lee, T.-W. (2008). Subcortical processes of motor response inhibition during a stop signal task. *Neuroimage*, *41*(4), 1352–1363.

Li, S., Jin, J.-N., Wang, X., Qi, H.-Z., Liu, Z.-P., & Yin, T. (2017). Theta and alpha oscillations during the retention period of working memory by rtms stimulating the parietal lobe. *Frontiers in behavioral neuroscience*, *11*, 170.

Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences*, *106*(24), 9925–9930. doi: 10.1073/pnas.0902262106

Liu, X., Banich, M. T., Jacobson, B. L., & Tanabe, J. L. (2004). Common and distinct neural substrates of attentional control in an integrated Simon and spatial Stroop task as assessed by event-related fMRI. *NeuroImage*, *22*(3), 1097–1106. doi: 10 .1016/j.neuroimage.2004.02.033

Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically possible and impossible actions: Effects of priming movements versus goals. *Journal of Experimental Psychology: Human Perception and Performance*, *34*(2), 489.

Los, S. A. (1996). On the origin of mixing ccosts: Exploring information processing in pure and mixed blocks of trials. *Acta Psychologica*, *94*, 145–188.

Lu, C.-H., & Proctor, R. W. (1995). The influence of irrelevant location information on performance: A review of the simon and spatial stroop effects. *Psychonomic bulletin & review*, *2*(2), 174–207.

Luber, B., Kinnunen, L. H., Rakitin, B. C., Ellsasser, R., Stern, Y., & Lisanby, S. H. (2007). Facilitation of performance in a working memory task with rTMS stimulation of the precuneus: Frequency- and time-dependent effects. *Brain Research*, *1128*(1), 120–129. doi: 10.1016/j.brainres.2006.10.011

Ma, Q., & Shang, Q. (2013). The influence of negative emotion on the simon effect as reflected by p300. *The Scientific World Journal*, *2013*, 6.

MacDonald, P. A., MacDonald, A. A., Seergobin, K. N., Tamjeedi, R., Ganjavi, H., Provost, J. S., & Monchi, O. (2011). The effect of dopamine therapy on ventral and dorsal striatum-mediated cognition in Parkinson's disease: Support from functional MRI. *Brain*, *134*(5), 1447–1463. doi: 10.1093/brain/awr075

Mansfield, K. L., van der Molen, M. W., Falkenstein, M., & van Boxtel, G. J. M. (2013). Temporal dynamics of interference in Simon and Eriksen tasks considered within the context of a dual-process model. *Brain and Cognition*, *82*(3), 353–363. doi: 10.1016/j.bandc.2013.06.001

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of eeg-and meg-data. *Journal of neuroscience methods*, *164*(1), 177–190.

Masaki, H., Takasawa, N., & Yamazaki, K. (2000). An electrophysiological study of the locus of the interference effect in a stimulus-response compatibility paradigm. *Psychophysiology*, *37*(4), 464–472.

Matsumoto, E., Misaki, M., & Miyauchi, S. (2004). Neural mechanisms of spatial stimulus-response compatibility: The effect of crossed-hand position. *Experimental Brain Research*, *158*(1), 9–17. doi: 10.1007/s00221-004-1872-7

Maurer, U., Brem, S., Liechti, M., Maurizio, S., Michels, L., & Brandeis, D. (2015). Frontal midline theta reflects individual task performance in a working memory task. *Brain topography*, *28*(1), 127–134.

Mazaheri, A., Nieuwenhuis, I. L. C., Van Dijk, H., & Jensen, O. (2009). Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human Brain Mapping*, *30*(6), 1791–1800. doi: 10.1002/hbm.20763

Melara, R. D., Wang, H., Vu, K. P. L., & Proctor, R. W. (2008). Attentional origins of the Simon effect: Behavioral and electrophysiological evidence. *Brain Research*, *1215*, 147–159. doi: 10.1016/j.brainres.2008.03.026

Melcher, T., Weidema, M., Eenshuistra, R. M., Hommel, B., & Gruber, O. (2008). The neural substrate of the ideomotor principle: An event-related fMRI analysis. *NeuroImage*, *39*(3), 1274–1288. doi: 10.1016/j.neuroimage.2007.09.049

Meltzoff, A. N., & Moore, M. K. (1989). Imitation in newborn infants: Exploring the range of gestures imitated and the underlying mechanisms. *Developmental psychology*, *25*(6), 954.

Mengotti, P., Corradi-Dell'Acqua, C., & Rumiati, R. I. (2012). Imitation components in the human brain: An fMRI study. *NeuroImage*, *59*(2), 1622–1630. doi: 10.1016/j.neuroimage.2011.09.004

Mengotti, P., Ticini, L. F., Waszak, F., Schütz-Bosbach, S., & Rumiati, R. I. (2013). Imitating others' actions: transcranial magnetic stimulation of the parietal opercula reveals the processes underlying automatic imitation. *European Journal of Neuroscience*, *37*(2), 316–322.

Mewaldt, S. P., Connelly, C. L., & Simon, R. (1980). Response selection in choice reaction time: test of a buffer model. *Memory & cognition*, *8*(6), 606–611.

Miller, N. E., & Dollard, J. (1941). Social learning and imitation.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). *Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies* (Vol. 36) (No. 1). doi: 10.1016/j.neubiorev.2011.07.004

Mosher, J. C., Leahy, R. M., & Lewis, P. S. (1999). EEG and MEG: Forward solutions for inverse methods. *IEEE Transactions on Biomedical Engineering*, *46*(3), 245–259. doi: 10.1109/10.748978

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. *Current Biology*, *20*(8), 750–756. doi: 10.1016/j.cub.2010.02.045

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, *41*(1), 152–156. doi: 10.1046/j.1469-8986.2003.00129.x

Muthukumaraswamy, S. D., & Singh, K. D. (2008). Modulation of the human mirror neuron system during cognitive activity. *Psychophysiology*, *45*(6), 896–905. doi: 10.1111/j.1469-8986.2008.00711.x

Neal, D. T., & Chartrand, T. L. (2011). Embodied emotion perception: amplifying and dampening facial feedback modulates emotion perception accuracy. *Social Psychological and Personality Science*, *2*(6), 673–678.

Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*(May), 1–11. doi: 10.3389/fnhum.2012.00127

Newman-Norlund. (2010). Virtual lesions of the IFG abolish response facilitation for biological and non-biological cues. *Frontiers in Behavioral Neuroscience*, *4*(03), 1–7. doi: 10.3389/neuro.08.005.2010

Newman-Norlund, R. D., Van Schie, H. T., Van Zuijlen, A. M., & Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative action. *Nature Neuroscience*, *10*(7), 817–818. doi: 10.1038/nn1911

Nicoletti, R., & Umilta, C. (1985). Responding with hand and foot: The right/left prevalence in spatial compatibility is still present. *Perception & Psychophysics*, *38*(3), 211–216. doi: 10.3758/BF03207147

Nigbur, R., Cohen, M. X., Ridderinkhof, K. R., & Stürmer, B. (2012). Theta dynamics reveal domain-specific control over stimulus and response conflict. *Journal of Cognitive Neuroscience*, *24*(5), 1264–1274.

Nigbur, R., Ivanova, G., & Stürmer, B. (2011). Theta power as a marker for cognitive

interference. *Clinical Neurophysiology*, *122*(11), 2185–2194. doi: 10.1016/j.clinph .2011.03.030

Nolte, G. (2003). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine & Biology*, *48*(22), 3637.

Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: A link between action observation and social skills. *Social Cognitive and Affective Neuroscience*, *2*(1), 62–66. doi: 10.1093/scan/nsl022

Obleser, J., & Weisz, N. (2012). Suppressed alpha oscillations predict intelligibility of speech and its acoustic details. *Cerebral Cortex*, *22*(11), 2466–2477. doi: 10.1093/ cercor/bhr325

Olk, B., Chang, E., Kingstone, A., & Ro, T. (2005). Modulation of antisaccades by transcranial magnetic stimulation of the human frontal eye field. *Cerebral Cortex*, *16*(1), 76–82.

Oostenbroek, J., Suddendorf, T., Nielsen, M., Redshaw, J., Kennedy-Costantini, S., Davis, J., ... Slaughter, V. (2016). Comprehensive longitudinal study challenges the existence of neonatal imitation in humans. *Current Biology*, *26*(10), 1334–1338.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*. doi: 10.1155/2011/156869

Park, H., Kim, J. S., & Chung, C. K. (2013). Differential beta-band event-related desynchronization during categorical action sequence planning. *PLoS One*, *8*(3), e59544.

Pellicano, A., Lugli, L., Baroni, G., & Nicoletti, R. (2009). The Simon effect with conventional signals a time-course analysis. *Experimental Psychology*, *56*(4), 219–227. doi: 10.1027/1618-3169.56.4.219

Perry, A., & Bentin, S. (2010). Does focusing on hand-grasping intentions modulate electroencephalogram μ and α suppressions? *Neuroreport*, *21*(16), 1050–1054.

Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved

in social interaction - Evidence from mu and alpha EEG suppression. *NeuroImage*, *58*(3), 895–904. doi: 10.1016/j.neuroimage.2011.06.060

Peterson, B. S., Kane, M. J., Alexander, G. M., Lacadie, C., Skudlarski, P., Leung, H. C., ... Gore, J. C. (2002). An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Cognitive Brain Research*, *13*(3), 427–440. doi: 10.1016/S0926-6410(02)00054-X

Petroni, A., Baguear, F., & Della-Maggiore, V. (2010). Motor resonance may originate from sensorimotor experience. *Journal of neurophysiology*, *104*(4), 1867–1871.

Phillips, J. M., Vinck, M., Everling, S., & Womelsdorf, T. (2014). A long-range fronto-parietal 5- to 10-Hz network predicts "top-down" controlled guidance in a task-switch paradigm. *Cerebral Cortex*, *24*(8), 1996–2008. doi: 10.1093/cercor/bht050

Pineda, J. A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Research Reviews*, *50*(1), 57–68.

Pineda, J. A., Allison, B. Z., & Vankov, A. (2000). The effects of self-movement, observation, and imagination on μ rhythms and readiness potentials (RP'S): Toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation Engineering*, *8*(2), 219–222. doi: 10.1109/86.847822

Pineda, J. A., Giromini, L., Soghoyan, G., Bohm, M., Maryanovsky, D., Zennaro, A., et al. (2018). Effects of repetitive transcranial magnetic stimulation (rtms) on attribution of movement to ambiguous stimuli and eeg mu suppression. *Brain research*, *1680*, 69–76.

Pobric, G., & Hamilton, A. F. d. C. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology*, *16*(5), 524–529.

Pogosyan, A., Gaynor, L. D., Eusebio, A., & Brown, P. (2009). Boosting Cortical Activity at Beta-Band Frequencies Slows Movement in Humans. *Current Biology*, *19*(19), 1637–1641. doi: 10.1016/j.cub.2009.07.074

Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Cognitive Brain Research*, *25*(3), 632–640. doi: 10.1016/j.cogbrainres

.2005.08.020

Press, C., Catmur, C., Cook, R., Widmann, H., Heyes, C., & Bird, G. (2012). fMRI Evidence of 'Mirror' Responses to Geometric Shapes. *PLoS ONE*, *7*(12), 1–10. doi: 10.1371/journal.pone.0051934

Press, C., Cook, J., Blakemore, S.-J., & Kilner, J. (2011). Dynamic Modulation of Human Motor Activity When Observing Actions. *Journal of Neuroscience*, *31*(8), 2792–2800.

Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1625), 2509–2514. doi: 10.1098/rspb.2007.0774

Press, C., Weiskopf, N., & Kilner, J. M. (2012). Dissociable roles of human inferior frontal gyrus during action execution and observation. *NeuroImage*, *60*(3), 1671–1677. doi: 10.1016/j.neuroimage.2012.01.118

Prinz, W. (1990). A common coding approach to perception and action. In *Relationships between perception and action* (pp. 167–201). Springer.

Proctor, R. W. (2011). Playing the simon game: Use of the simon task for investigating human information processing. *Acta Psychologica*, *136*(2), 182–188.

Proctor, R. W., & Fisicaro, S. A. (1977). Time, capacity, and selection between perceptual attributes. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(2), 337–348. doi: 10.1037/0096-1523.3.2.337

Proctor, R. W., & Lu, C. H. (1994). Referential coding and attention-shifting accounts of the Simon effect. *Psychological Research*, *56*(3), 185–195. doi: 10.1007/BF00419706

Proctor, R. W., Miles, J. D., & Baroni, G. (2011). Reaction time distribution analysis of spatial correspondence effects. *Psychonomic Bulletin & Review*, *18*(2), 242–266. doi: 10.3758/s13423-011-0053-5

Proctor, R. W., & Pick, D. F. (2003). Display-control arrangement correspondence and logical recoding in the Hedge and Marsh reversal of the Simon effect. *Acta*

Psychologica, *112*(3), 259–278. doi: 10.1016/S0001-6918(02)00125-7

Proctor, R. W., & Vu, K. P. L. (2002). Mixing location-irrelevant and location-relevant trials: Influence of stimulus mode on spatial compatibility effects. *Memory and Cognition*, *30*(2), 281–293. doi: 10.3758/BF03195289

Ratcliff, R. (1979). Group reaction time distributions and an analysis of distribution statistics. *Psychological Bulletin*, *86*(3), 446–461. doi: 10.1037/0033-2909.86.3.446

Ridderinkhof, K. R., van den Wildenberg, W. P. M., Wijnen, J., & Burle, B. (2004). Response Inhibition in Conflict Tasks Is Revealed in Delta Plots. *Cognitive neuroscience of attention*, 369–377.

Ridderinkhof, R. K. (2002). Micro-and macro-adjustments of task set: activation and suppression in conflict tasks. *Psychological research*, *66*(4), 312–323.

Rizzolatti, G., & Craighero, L. (2004). The Mirror-Neuron System. *Annual Review of Neuroscience*, *27*(1), 169–192. doi: 10.1146/annurev.neuro.27.070203.144230

Roux, F., & Uhlhaas, P. J. (2014). *Working memory and neural oscillations: Alpha-gamma versus theta-gamma codes for distinct WM information?* (Vol. 18) (No. 1). doi: 10.1016/j.tics.2013.10.010

Ruysschaert, L., Warreyn, P., Wiersema, J. R., Oostra, A., & Roeyers, H. (2014). Exploring the Role of Neural Mirroring in Children with Autism Spectrum Disorder. *Autism Research*, *7*(2), 197–206. doi: 10.1002/aur.1339

Sack, A. T. (2009). Parietal cortex and spatial cognition. *Behavioural brain research*, *202*(2), 153–161.

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1015–1022. doi: 10.1016/j.neubiorev.2009.12.006

Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., & Hanslmayr, S. (2005). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Human Brain Mapping*, *26*(2), 148–155. doi: 10.1002/hbm.20150

Sauser, E. L., & Billard, A. G. (2006). Parallel and distributed neural models of the ideomotor principle: An investigation of imitative cortical pathways. *Neural Networks*, *19*(3), 285–298.

Scerrati, E., Lugli, L., Nicoletti, R., & Umiltà, C. (2017). Comparing Stroop-like and Simon Effects on Perceptual Features. *Scientific Reports*, *7*(1), 1–11. doi: 10.1038/s41598-017-18185-1

Scheutz, M., & Bertenthal, B. I. (2012). A Computational PDP Model for Explaining Automatic Imitation. *Cognitive Science*, *17*, 2288–2293.

Sebastiani, V., de Pasquale, F., Costantini, M., Mantini, D., Pizzella, V., Romani, G. L., & Della Penna, S. (2014). Being an agent or an observer: Different spectral dynamics revealed by MEG. *NeuroImage*, *102*(P2), 717–728. doi: 10.1016/j.neuroimage.2014.08.031

Seger, C. A. (2005). The Roles of the Caudate Nucleus in Human Classification Learning. *Journal of Neuroscience*, *25*(11), 2941–2951. doi: 10.1523/JNEUROSCI.3401-04.2005

Shadmehr, R., & Holcomb, H. H. (1999). Inhibitory control of competing motor memories. *Experimental Brain Research*, *126*(2), 235–251. doi: 10.1007/s002210050733

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal Synchronization along the Dorsal Visual Pathway Reflects the Focus of Spatial Attention. *Neuron*, *60*(4), 709–719. doi: 10.1016/j.neuron.2008.09.010

Silva, F. L. (2013). Eeg and meg: relevance to neuroscience. *Neuron*, *80*(5), 1112–1128.

Simon, J. R. (1969). Reactions torward the source of stimulation. *J. ˜of Experimental Psychology*, *81*(1), 174–176.

Simon, J. R., & Acosta, E. (1982). Effect of irrelevant information on the processing of relevant information: Facilitation and/or interference? The influence of experimental design. *Perception & Psychophysics*, *31*(4), 383–388. doi: 10.3758/BF03202663

Simon, J. R., Acosta, E., Mewaldt, S. P., & Speidel, C. R. (1976). The effect of an irrelevant directional cue on choice reaction time: Duration of the phenomenon and

its relation to stages of processing. *Perception & Psychophysics*, *19*(1), 16–22. doi: 10.3758/BF03199380

Simon, J. R., Craft, J. L., & Webster, J. B. (1973). Reactions toward the stimulus source: Analysis of correct responses and errors over a five-day period. *Journal of Experimental Psychology*, *101*(1), 175–178. doi: 10.1037/h0035766

Simpson, E. A., Murray, L., Paukner, A., & Ferrari, P. F. (2014). The mirror neuron system as revealed through neonatal imitation: Presence from birth, predictive power and evidence of plasticity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1644). doi: 10.1098/rstb.2013.0289

Smith, A. (1976). *The theory of moral sentiments: The glasgow edition of the works and correspondence of adam smith*. Oxford University Press UK.

Stel, M., van Dijk, E., & van Baaren, R. B. (2016). When and Why Mimicry is Facilitated and Attenuated. *Social and Personality Psychology Compass*, *10*(10), 561–574. doi: 10.1111/spc3.12269

Stel, M., & Vonk, R. (2010). Mimicry in social interaction: Benefits for mimickers, mimickees, and their interaction. *British Journal of Psychology*, *101*(2), 311–323. doi: 10.1348/000712609X465424

Stock, A., & Stock, C. (2004). A short history of ideo-motor action. *Psychological Research*, *68*(2-3), 176–188. doi: 10.1007/s00426-003-0154-5

Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence Effects with Manual Gestures and Postures: A Study of Imitation. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(6), 1746–1759. doi: 10.1037/0096-1523.26.6.1746

Suetsugi, M., Mizuki, Y., Ushijima, I., Kobayashi, T., Tsuchiya, K., Aoki, T., & Watanabe, Y. (2000). Appearance of frontal midline theta activity in patients with generalized anxiety disorder. *Neuropsychobiology*, *41*(2), 108–112. doi: 10.1159/000026641

Tagliabue, M., Zorzi, M., Umiltà, C., & Bassignani, F. (2000). The role of long-term-memory and short-term-memory links in the Simon effect. *Journal of Experimental*

Psychology: Human Perception and Performance, *26*(2), 648–670. doi: 10.1037/0096-1523.26.2.648

Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The Human Premotor Cortex Is 'Mirror' only for Biological Actions. *Current Biology*, *14*(2), 117–120. doi: 10.1016/j.cub.2004.01.005

Tamura, T., Gunji, A., Takeichi, H., Shigemasu, H., Inagaki, M., Kaga, M., & Kitazaki, M. (2012). Audio-vocal monitoring system revealed by mu-rhythm activity. *Frontiers in Psychology*, *3*(07), 1–10. doi: 10.3389/fpsyg.2012.00225

Taulu, S., & Simola, J. (2006). Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. *Physics in Medicine and Biology*, *51*(7), 1759–1768. doi: 10.1088/0031-9155/51/7/008

Thorpe, S. G., Cannon, E. N., & Fox, N. A. (2016). Rhythms From Infancy Through Adulthood. *Journal of Clinical Neurophysiology*, *127*(1), 254–269. doi: 10.1016/j.clinph.2015.03.004.

Tidoni, E., Borgomaneri, S., Di Pellegrino, G., & Avenanti, A. (2013). Action simulation plays a critical role in deceptive action recognition. *Journal of Neuroscience*, *33*(2), 611–623.

Tkach, D., Reimer, J., & Hatsopoulos, N. G. (2007). Congruent activity during action and action observation in motor cortex. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *27*(48), 13241–13250. doi: 10.1523/JNEUROSCI.2895-07.2007

Tucker, M., & Ellis, R. (1998). On the Relations between Seen Objects and Components of Potential Actions. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 830–846. doi: 10.1037/0096-1523.24.3.830

Tzagarakis, C., Ince, N. F., Leuthold, A. C., & Pellizzer, G. (2010). Beta-Band Activity during Motor Planning Reflects Response Uncertainty. *Journal of Neuroscience*, *30*(34), 11270–11277. doi: 10.1523/JNEUROSCI.6026-09.2010

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix,

N., ... Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*(1), 273–289. doi: 10.1006/nimg.2001.0978

Ubaldi, S., Barchiesi, G., & Cattaneo, L. (2013). Bottom-up and top-down visuomotor responses to action observation. *Cerebral Cortex*, *25*(4), 1032–1041.

Umiltà, C., & Zorzi, M. (1997). Commentary on barber and o'leary: Learning and attention in sr compatibility. *Advances in psychology*, *118*, 173–178.

Urgen, B. A., Plank, M., Ishiguro, H., Poizner, H., & Saygin, A. P. (2013). EEG theta and Mu oscillations during perception of human and robot actions. *Frontiers in Neurorobotics*, *7*(NOV), 1–13. doi: 10.3389/fnbot.2013.00019

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *Journal of Neuroscience*, *27*(30), 8023–8030.

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature neuroscience*, *10*(1), 30.

Valle-Inclán, F. (1996). The locus of interference in the Simon effect: An ERP study. *Biological Psychology*, *43*(2), 147–162. doi: 10.1016/0301-0511(95)05181-3

Van Baaren, R., Janssen, L., Chartrand, T. L., & Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2381–2389. doi: 10.1098/rstb.2009.0057

van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Research Report Mimicry and Prosocial Behavior. *Psychological Science (Wiley-Blackwell)*, *15*(1), 71–74.

van Baaren, R. B., Holland, R. W., Steenaert, B., & van Knippenberg, A. (2003). Mimicry for money: Behavioral consequences of imitation. *Journal of Experimental Social Psychology*, *39*(4), 393–398. doi: 10.1016/S0022-1031(03)00014-3

Van Elk, M., Van Schie, H. T., & Bekkering, H. (2011). Imitation of hand and tool

actions is effector-independent. *Experimental Brain Research*, *214*(4), 539–547. doi: 10.1007/s00221-011-2852-3

Vannuscorps, G., & Caramazza, A. (2016). Typical action perception and interpretation without motor simulation. *Proceedings of the National Academy of Sciences*, *113*(1), 86–91.

VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience*, *13*(4), 454–461. doi: 10.1162/08989290152001880

Van Veen, B. D., Van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Transactions on biomedical engineering*, *44*(9), 867–880.

Van Veen, V., & Carter, C. S. (2005). Separating semantic conflict and response conflict in the Stroop task: A functional MRI study. *NeuroImage*, *27*(3), 497–504. doi: 10.1016/j.neuroimage.2005.04.042

van Wijk, B., Beek, P. J., & Daffertshofer, A. (2012). Neural synchrony within the motor system: what have we learned so far? *Frontiers in human neuroscience*, *6*, 252.

Vigário, R., Jousmäki, V., Hämäläinen, M., Hari, R., & Oja, E. (1998). Independent component analysis for identification of artifacts in magnetoencephalographic recordings. In *Advances in neural information processing systems* (pp. 229–235).

Vigneswaran, G., Philipp, R., Lemon, R. N., & Kraskov, A. (2013). M1 corticospinal mirror neurons and their role in movement suppression during action observation. *Current Biology*, *23*(3), 236–243. doi: 10.1016/j.cub.2012.12.006

Vink, M., Kahn, R. S., Raemaekers, M., Van Den Heuvel, M., Boersma, M., & Ramsey, N. F. (2005). Function of striatum beyond inhibition and execution of motor responses. *Human Brain Mapping*, *25*(3), 336–344. doi: 10.1002/hbm.20111

Vu, K. P. L., Proctor, R. W., & Urcuioli, P. (2003). Transfer effects of incompatible location-relevant mappings on a subsequent visual or auditory Simon task. *Memory and Cognition*, *31*(7), 1146–1152. doi: 10.3758/BF03196135

Walsh, V., & Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. *Nat Rev Neurosci*, *1*(1), 73–80. doi: 10.1038/35036239

Wang, K., Li, Q., Zheng, Y., Wang, H., & Liu, X. (2014). Temporal and spectral profiles of stimulus-stimulus and stimulus-response conflict processing. *NeuroImage*, *89*, 280–288. doi: 10.1016/j.neuroimage.2013.11.045

Wang, W., Viswanathan, S., Lee, T., & Grafton, S. T. (2016). Coupling between theta oscillations and cognitive control network during cross-modal visual and auditory attention: Supramodal vs modality-specific mechanisms. *PLoS ONE*, *11*(7), 1–16. Retrieved from `http://dx.doi.org/10.1371/journal.pone.0158465` doi: 10.1371/journal.pone.0158465

Wang, Y., & Hamilton, A. F. D. C. (2012). Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. *Frontiers in human neuroscience*, *6*(06), 153. doi: 10.3389/fnhum.2012.00153

Wheeler, L. (1966). Toward a theory of behavioral contagion. *Psychological Review*, *73*(2), 179–192. doi: 10.1037/h0023023

Wiegand, K., & Wascher, E. (2005). Dynamic aspects of stimulus-response correspondence: evidence for two mechanisms involved in the simon effect. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(3), 453.

Wiegand, K., & Wascher, E. (2007). Response coding in the Simon task. *Psychological Research*, *71*(4), 401–410. doi: 10.1007/s00426-005-0027-1

Wood, A., Rychlowska, M., Korb, S., & Niedenthal, P. (2016). Fashioning the face: sensorimotor simulation contributes to facial expression recognition. *Trends in cognitive sciences*, *20*(3), 227–240.

Woodman, G. F. (2010). A brief introduction to the use of event-related potentials (ERPs) in studies of perception and attention. *Attention and Perceptual Psychophysiology*, *72*(8), 1–29. doi: 10.3758/APP.72.8.2031.A

Wurm, M. F., & Schubotz, R. I. (2012). Squeezing lemons in the bathroom: Contextual information modulates action recognition. *NeuroImage*, *59*(2), 1551–1559. doi:

10.1016/j.neuroimage.2011.08.038

Yang, F.-c., Jacobson, T. K., & Burwell, R. D. (2017). Single neuron activity and theta modulation in the posterior parietal cortex in a visuospatial attention task. *Hippocampus*, *27*(3), 263–273. doi: 10.1002/hipo.22691

Zaepffel, M., Trachel, R., Kilavik, B. E., & Brochier, T. (2013). Modulations of EEG Beta Power during Planning and Execution of Grasping Movements. *PLoS ONE*, *8*(3). doi: 10.1371/journal.pone.0060060

Zhang, H. H., Zhang, J., & Kornblum, S. (1999). A parallel distributed processing model of stimulus–stimulus and stimulus–response compatibility. *Cognitive psychology*, *38*(3), 386–432.

Zhang, J., & Kornblum, S. (1997). Distributional analysis and de jong, liang, and lauber's (1994) dual-process model of the simon effect. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(5), 1543.

Zhang, Y., Chen, Y., Bressler, S. L., & Ding, M. (2008). Response preparation and inhibition: the role of the cortical sensorimotor beta rhythm. *Neuroscience*, *156*(1), 238–246.

Zhao, J., Liang, W. K., Juan, C. H., Wang, L., Wang, S., & Zhu, Z. (2015). Dissociated stimulus and response conflict effect in the Stroop task: Evidence from evoked brain potentials and brain oscillations. *Biological Psychology*, *104*, 130–138. doi: 10.1016/j.biopsycho.2014.12.001

Zhou, B., Zhang, J. X., Tan, L. H., & Han, S. (2004). Spatial congruence in working memory: an ERP study. *Neuroreport*, *15*(18), 2795–2799.