The Control of Mimicry by Social Signals

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Abstract

One remarkable feature of social interactions is spontaneous mimicry. People have a tendency to unconsciously imitate other's behaviours. This mimicry increases liking and affiliation between individuals and plays an important role in social cognition. Though mimicry is not normally consciously controlled, past research suggests that people mimic differently across social situations. In order to better understand the flexibility of mimicry in socal contexts, this thesis examined how social signals impact on mimicry by using a cognitive approach. Four behavioural studies consistently suggest that mimicry is subtly and strategically controlled by social signals. Specifically, in the first study we found that eye gaze is a powerful controlling signal on mimicry. Direct gaze rapidly and specifically enhances mimicry of intransitive hand movements. In the second study, we clarified that this eye contact effect on mimicry is not due to any arousal or attentional effect, but is driven by the social cue of direct gaze. In the third study, we found a joint effect of likeability and social status on mimicry. These two features interact in driving mimicry and optimize the affiliative function of mimicry in social interaction. Finally in the fourth study, we found that mimicry is sensitive to social primes. Prosocial and antisocial primes subtly modulate mimicry according to the self-relatedness of the primes.

To further investigate the neural mechanism of the sutble control of mimicry by social signals, functional magnetic resonance imaging was used to examine the effect of eye contact on mimicry. The results showed that two key brain systems for social cognition—medial prefrontal cortex (mPFC) and mirror neuron system (MNS)—work together to control mimicry on line in

social contexts. In particular, dynamic causal modelling analysis revealed that mPFC is the originator of the eye contact effect on mimicry and this region modulates the sensory inputs to the MNS according to gaze directions. These findings suggest that mPFC plays a key role in the strategic control of mimicry in social contexts.

All experiments are then discussed in relation to current theories of mimicry. We suggest that this subtle and strategic control of mimicry is essential to human competence in social interactions and is important for our understanding of why and how people mimic.

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Chapter 1. Introduction

"Each of us is in fact what he is almost exclusively by virtue of his imitativeness" —

William James (1890, p. 741)

One striking phenomenon of human social interactions is spontaneous mimicry. People have a tendency to unconsciously copy other's actions, mannerisms, facial expressions, languages and other behaviours (Chartrand and Bargh, 1999). We start to yawn upon seeing someone else yawning and start to frown when seeing others frowning. We whisper to someone who is whispering and speak much louder when others do so. We walk slower in the presence of the elderly but scurry when centered by busy people in the London underground. Apparently, human mimicry is ubiquitous.

In the past 20 years, this spontaneous mimicry becomes the key focus of research in social psychology and cognitive neuroscience (Heyes, 2009). Investigations on the causes, consequences and underlying mechanisms of mimicry have been widely carried out in these two disciplines, but with different perspectives. Specifically, by using naturalistic paradigms, social psychology focuses on the visible mimicry behaviours during social interaction and how these mimicry behaviours change across different social contexts; whereas in cognitive neuroscience, researchers primarily adopt simple, well-controlled lab tasks to examine the underlying mirroring mechanism and to establish cognitive models of mimicry process. Here in the first chapter, I will systematically review past research on mimicry in these two disciplines and then give an overview of the questions the thesis will address.

1.1 Mimicry in Social Psychology

As William James noted in the opening quote, the phenomenon that individuals imitate the behaviours of others has long been of interest to psychologists (e.g., James, 1890). The past thirty years, in particular in social psychology, has seen a surge of research exploring the unconscious side of imitation in which people subtly and spontaneously imitate their social interaction partners, including mimicry of physical movements, speech patterns, facial expressions and emotions. This unconscious side of imitation is defined as mimicry, and is suggested to be essential for social communication and affiliation. It is notably different from the conscious imitation, which is often regarded as an important part of social learning theory and culture inheritance (Heyes, 2009).

To better understand what we mimic, how we mimic and why we mimic, systematic investigations into the wide ranging consequences of mimicry have been conducted in social psychology, as well as investigations into social factors that facilitate and inhibit mimicry. In light of these trends, the current section will unfold in the following manner: first, I will introduce the close link between perception and behaviour (see 1.1.2) and briefly review representative evidence of mimicry behaviour in the literature of social psychology (see 1.1.3); next, I will discuss the social importance of mimicry by reviewing the consequences and moderators of it (see 1.1.4 and 1.1.5); finally, I will discuss different theoretical approaches to the question of why we mimic. (see 1.1.6)

1.1.1 Methodologies

At the beginning of the review, it is necessary to overview the methodologies that have been commonly used in the investigation of mimicry behaviour. Generally speaking, social psychologists adopt naturalistic paradigms to investigate visible mimicry behaviours. Participants are often asked to complete a social task with an unknown confederate in a natural setting. The social task is usually simple but very interactive, for example, participant are required to describe the features of some photos in magazines (the 'photo description task', Chartrand and Bargh, 1999), which aims to make participants fully engaging in the interaction with the confederate and being unaware of their own behaviours. Crucially, the confederate's behavioural patterns during the interaction were manipulated by the researchers and hidden video cameras were used to record participant's corresponding behaviours throughout the whole interaction. For example, in Chartrand and Bargh (1999, experiment 1), confederates were trained to subtly perform or not perform a featured action during interaction with the participant (e.g. face touch or foot shake) and the whole interactions were recorded. Then coders blind to the experimental condition and hypotheses later watched these recordings and counted the amount of face touching and foot shaking that the participant engaged in. By comparing manipulations with or without featured actions performed by the confederates, researchers revealed that the featured action was substantially mimicked by the participants.

Similarly, in studies of investigating consequences of mimicry (e.g. Chartrand and Bargh, 1999, experiment 2), confederates were trained to

subtly copy or not copy the postures and mannerisms of the participant throughout the interaction. Participants were then asked to rate the smoothness of the social interaction and the likeability of the confederate by a questionnaire. Again, by comparing the ratings between manipulations with and without mimicry, researchers found that mimicry significantly enhances liking between participants and confederates and facilitate the social interaction.

When it comes to the investigations of modulators of mimicry, another naturalistic approach called 'subliminal priming' is used when introducing social modulators. Subliminal priming is an implicit memory effect in which exposure to a pre-stimulus influences response to a later stimulus. It can occur following perceptual, semantic, or conceptual stimulus repetition. It happens, for example, that if a person observe prosocial behaviour, or read a list of prosocial words (e.g. 'helping', 'together', 'cooperation') or complete scrambled sentences including prosoical words (i.e. the 'scrambled sentence task', Srull and Wyer, 1979), the probability that they later behave in a prosocial way is greater than if not so primed (Over and Carpenter, 2009b; Lakin and Chartrand, 2003; Leighton et al., 2010). Another example is when people experienced a social exclusion in a virtual video game or watched someone being ostracized, they later behave like being ostracized in real social interactions (Lakin et al., 2008; Over and Carpenter, 2009a). By using subliminal priming, researchers are able to examine whether a motive, an attitude or some features of a person can modulate one's tendency to mimic.

Back to the main topic of the thesis, in the next section I will introduce a close link between perception and behaviour on which mimicry is grounded. I

will present evidence suggesting that one's own behaviour is profoundly influenced by the contexts, conspecifics and others' behaviours. I will stress the notion that perception is for behaviour—it is the best guidance and control device for one's social behaviour.

1.1.2 Perception-Behaviour Link

Perception and behaviour are two interdependent components of cognition. Psychology used to believe that the most important function of perception is to understand the world: we perceive because we want to know what is going on around us. Although this answer is straight-forward, it is also largely incomplete, and to some extent wrong. Certainly, perception is essential for us to comprehend our environment, but that does not mean that this understanding is the reason that we are evolved to obtain this function. Rather, understanding is a means by which we act effectively (Dijksterhuis and Bargh, 2001). Adaptive perception is ultimately in the service of functional behavioural responding to the environment, and comprehension and understanding are only important means to that end (Milner and Goodale, 1995). Therefore, perception is for doing: it is our best action guidance and control device.

This perspective on action and perception has been widely supported by biological research in non-primate animals where there are multiple direct one-to-one relations between a specific perceptual process and a specific from of action. Frogs, for instance, have two different perceptual systems (Ingle, 1973). One system is responsible for detecting and hunting small prey objects whereas the other is responsible for avoiding large objects. Thus for a

frog, a large object above the surface means "flight", while a small, irregularly moving object on the surface means "go for it". There are no exceptions: the perception of a small object on the surface always prompts hunting behaviour and the perception of a large object always prompts avoidance. Further animal evidence for the direct relation between perception and action comes from studies of the group behaviour of fish and birds. Fish in shoals (and also migrating birds) often display impressive synchrony of movement: they all move in the same direction and then change direction at the same time. Substantial evidence suggests that if a fish perceives the fellow fish in front of it change direction, it can do nothing but the same (Pitcher, 1979).

For humans, we have a behavioural repertoire that is more flexible than that of frogs, fish and birds. However, this primitive perception-behaviour link is still preserved in humans' more complex social behaviour. What people are about to do is profoundly influenced by what they just perceived. This guidance of perception on behaviour helps individuals conform to the rules of the society and coordinate with other members of the society. Before I review this evidence, it is necessary to raise another important issue at first: what does a human perceiver perceive? First of all, human perceivers perceive the environment surrounding them and context information at that time point: we know when and where we are. Second, we perceive our conspecifics: we meet elders and youths, men and women, strangers and acquaintances and ingroups and outgroups. Finally, we perceive 'specific observable behaviours'. It involves behaviours that we can literally perceive. We perceive gestures and movements of others: we can see someone wave, yawn, scratch the head or shake the foot. We can perceive various facial expressions and emotions: we

see people smile, angry or fear. Also, we hear people speak: we perceive the contents of speech (words and syntax) as well as accents and tone of voice. Social psychologists have demonstrated that behaviour can be automatically influenced by all three forms of perception.

For the context information, researchers found that the mere perception of social settings affects one's actual behaviour. Aarts and Dijksterhuis (2003) primed participants with locations that were associated with situational norms. For example, some participants were primed with stimuli related to libraries, a location for which the norm is quiet behaviour. They found that those who were primed with the location or a goal to visit the location later behaved in ways that were consistent with the norm for that location. For instance, those who were exposed to photos of library subsequently recited a text passage in a significantly softer voice than non-primed participants. They explained that behavioural information can be activated from the mere perception of social settings or contexts and subsequently guide actual behaviour in the absence of people's intentions and awareness.

The evidence that behaviour can be influenced by the perception of our conspecifics is also abundant. We spontaneously generate trait inferences based on easily detectable identifying features of a person and meanwhile activate social stereotypes of the group that person belongs to (Gilbert, 1989; Winter and Uleman, 1984). These trait concepts and social stereotypes can dominate the perceiver's mindset and lead him/her to behave in a consistent way. Bargh et al. (1996) were the first to report the direct effects of trait concept and stereotype activation on behaviour. In one of their studies, participants were primed with trait concepts of either rudeness or politeness

by completing a 'scrambled sentence task' (see 1.1.1). Participants were requested to meet the experimenter in a different office upon finishing the task. When participants approached the experimenter, the experimenter was talking to a confederate. The confederate surreptitiously measured the time it took for participants likely to interrupt the conversation. They found that participants who were primed with rudeness were more likely to interrupt than were control participants, whereas participants primed with politeness were least likely to interrupt. This result suggests that activation of trait concepts elicits corresponding behaviour; activation of the trait rude makes us rude and activation of the trait polite makes us polite. In the next study, they replicated a consistent result on social stereotypes. Participants were seated behind a computer and were asked to engage in a very boring and tedious task. While engaging in this task, some participants were subliminally presented with photographs of male African-Americans whereas others were subliminally presented with male Caucasian faces. After participants had been performing the boring task for a while, the computer program beeped and displayed an error message of data saving. Subsequently the experimenter came to require participants to do the task again. The participants were videotaped during these moments and the dependent variable was the level of hostility participants displayed upon hearing that they had to start all over again. As the stereotype of African-Americans is often associated with hostility, researchers found that the reaction of the participants primed with the stereotype of African-Americans were rated as more hostile than the reaction of the participants primed with Caucasian faces. These findings demonstrate that the perception of members of a stereotyped group lead to corresponding

stereotypic behaviour.

Similar behavioural effects by trait and stereotype activation can also be found when participants perceive elderly people. For example, Bargh et al. (1996) used the scrambled sentence task to prime participants with words related to elderly people and then recorded the time it took participants to walk from the experimental room to the nearest elevator. As elderly are often associated with slowness, they found that participants primed with the elderly stereotype walked significantly slower than control participants. This result has later on been replicated by several other groups. In the experiment of Kawakami et al. (2002), some participants were exposed to various photographs of elderly people, whereas others were exposed to photographs of university students. The photographs were presented in a lexical decision task: each photograph was accompanied by a personality trait and the task of the participant was to decide whether the presented traits were descriptive of the social category displayed on the photograph (elderly vs. student). The data clearly showed that reaction latencies on decision task were longer when the words were preceded by a photograph of an elderly person than when the words were preceded by photographs of younger people. Dijksterhuis et al., (2001) obtained compatible results in a different paradigm. In their study, some participants were instructed to form an impression of various elderly individuals while looking at the photographs of these individuals. The second task, which was ostensibly unrelated to the first task, was a lexical decision task where participants were asked to decide as fast as possible whether words presented on the screen were existing words (car, shop) or random letter strings (ikn, geru). As expected, the results showed that participants

primed with the elderly stereotype showed reaction times that were considerably slower than participants who were not primed. In sum, these results suggest that people displayed behaviour (slowness or hostility) corresponding to the activated trait or stereotype of a group (elderly or African-Americans) and this perception-behaviour is totally out of awareness.

1.1.3 Evidence of Mimicry—the 'Chameleon Effect'

The main topic of this thesis comes from the direct link between behaviour and the third type of perception—the 'specific observable behaviours'. This link is often termed as 'Chameleon Effect', which first appeared in a seminal paper by Chartrand and Bargh (1999). In that paper, they defined mimicry as unconscious copying of the postures, mannerisms, facial expressions, speech style and other behaviours of one's interaction partners, such that one's behaviour passively and unintentionally changes to match that of others in one's current social environment. They suggested such a "chameleon effect" may manifest itself in three different ways—'motor mimicry' (e.g. crossing one's arms while talking with someone else who has his or her arms crossed), 'facial mimicry'' (e.g. starting yawning when seeing other people yawning) and 'speech mimicry' (e.g. using the idiosyncratic verbal expressions or speech inflections of a friend). Common to all three cases is that one typically does not notice doing these things-if at all-until after the fact.

Motor mimicry

Motor mimicry refers to the adoption of the postures, gestures, and motor movements of one's interaction partner. The evidence of motor mimicry can

be traced back to early anecdotes. For example, in Eidelberg's experiment (1929), participants played a game where they were instructed to point at their nose upon hearing the word "nose" and to point at a lamp upon hearing the word "lamp." The experimenter, who was clearly visible to the participants, also pointed at his or her nose or at the lamp upon hearing the corresponding instruction. After a while, the experimenter started to make "mistakes," in that he or she pointed at the lamp upon hearing the word nose and vice versa. Interestingly, participants started to make the same mistakes as well. They spontaneously imitated the gestures made by the experimenter, despite the instruction to follow the verbal cues (i.e., the words "nose" and "lamp") and not the behaviour of the experimenter.

Early studies by Bernieri and colleagues (1988) tested whether naive judges rated ''real'' interactions as more synchronous than interactions that never actually took place. To do this, researchers videotaped several mother–infant interactions, always with the mother on the right part of the screen and the infant on the left. They then created different versions of the videos in which mothers were sometimes paired with their own infants and sometimes with other infants. Participants watched these videos and rated how physically in synchronization the pairs were. Results clearly showed that mothers were judged to be more in sync with their own infants than with other infants. This finding suggests that a high level synchrony between interaction partners is a key feature of human social interaction.

Chartrand and Bargh (1999) were the first to systematically test the automaticity and specificity of motor mimicry in dyadic communication where two individuals reciprocally interact with each other. Participants engaged in a

'photo description task' (see 1.1.1) with two confederates one after another. The first confederate either moved her foot or touched her face throughout the session. The second confederate performed the behaviour the first did not do (for example, if the first confederate performed a foot shaking, then the second one performed a face touching). Hidden video cameras were used to record these sessions. Results revealed that participants changed their motor behaviours to match the actions they perceived in their current environment. That is, they moved their foot more when they were with the foot moving confederate than the face touching confederate, and they touched their face more when with the face toucher than the foot mover. Participants reported no awareness of either the confederates' actions or their own mimicry of those motor behaviours, providing evidence that motor mimicry is a spontaneous and unconscious process.

Facial mimicry

Facial mimicry is another recognizable form of human mimicry where people have the tendency to adopt the facial expressions (and corresponding elicited emotions) of others. Early investigators have studied facial mimicry among newborns and their mothers (Field et al., 1982; Meltzoff and Moore, 1977, 1983, 1989; Meltzoff, 1985, 1988; O'Toole and Dubin, 1968). Meltzoff and Moore (1977, 1983) showed that even one-month-old babies imitate facial expressions. If a mother looks at a baby and opens her mouth, the baby will open its mouth. If a mother sticks out her tongue, the baby will often do the same. However, this evidence is highly controversial (Jones, 2009; see 1.1.6). Interestingly, researchers also found that it is not always the baby who mimics the mother during the infant-mother interaction, facial mimicry can also be

observed from the mother side when they feed their infants a spoonful of food. O'Toole and Dubin (1968) reported that mothers tend to open their mouths in response to their infants opening their mouths to feed.

Another example of facial mimicry in adults is contagious yawning. If, after a long journey, a person starts to yawn, usually his or her travel companions start to yawn within a few minutes. This tendency to yawn triggered by perceiving others' yawning has been well documented in the literature (Platek et al., 2003; Provine, 1986, 1989; Senju et al., 2007). Provine (1986) asked participants to watch a five minute videotape. In one condition, participants watched a video with yawning people, whereas in a control condition participants watched a video with smiling people. As expected, 55% of the participants in the experimental (i.e., yawn) condition started to yawn while watching the video, as opposed to only 21% in the control (i.e., smile) condition.

Other evidence of facial mimicry comes from psychophysiological studies by Dimberg and colleagues. They used facial electromyography (EMG) to indicate that facial expressions elicit facial muscular activity congruent with the presented facial expressions. For example, Dimberg (1982) showed that mere photographic presentations of angry and happy facial expressions induced spontaneous corrugator supercilii muscle activity (brow lowering actions, prototypical in angry facial expressions) and zygomatic major muscle activity (lip corner pulling actions, prototypical in happy facial expressions), respectively. He claimed that this facial muscular activity may be interpretable as mimicry behaviour. Later, Dimberg, et al. (2000) reported that facial EMG activity occurred even without awareness of the specific facial expression,

confirming the spontaneous nature of the responses. In addition, facial mimicry occurs rapidly; Dimberg and Thunberg (1998) showed that facial EMG activity occurred after only 500ms of exposure to the facial pictures. These studies imply that facial muscle activity that may relate to facial mimicry occurs spontaneously and rapidly in response to facial expressions.

An interesting study recently conducted by Bailey and Henry (2009) suggests that facial mimicry is still preserved in older adulthood. Although old people have explicit visual recognition difficulties and cannot consciously perceive the facial emotion stimuli, facial EMG activity suggests that they still have intact facial mimicry to the angry and happy facial expression. This finding supports the pervasiveness and unconsciousness of facial mimicry, ranging from newborns to elders.

Speech mimicry

Finally, there is evidence of mimicry of speech related variables. Simner (1971) conducted research with infants and demonstrated that newborns as young as 2 to 4 days old will cry in response to another infant's crying. What is fascinating about Simner's research is the finding that infants do not mimic synthetic cries, suggesting that newborn infants can actually discriminate between real and artificial cries.

Research on mimicry of speech patterns conducted with adult participants has shown that speakers tend to adopt each other's accents, latency to speak, speech rate, and utterance duration (Cappella and Planalp, 1981; Giles and Powesland, 1975; Matarazzo and Wiens, 1972; Webb, 1969). Speakers also use the same syntax as their conversation partners. For example, in a study by Bock (1986; 1989), participants would hear and repeat

a sentence such as "The corrupt inspector offered a deal to the bar owner." Later, participants would see a picture of, for instance, a boy handing a valentine to a girl. This picture can be described as "The boy is handing a valentine to a girl" or as "The boy is handing the girl a valentine." As the first sentence has a similar syntactic form as the priming sentence, this is the description participants most often gave. Syntactic structures appear to carry over from one sentence to another.

Whereas in the studies conducted by Bock (1986) participants activated a particular syntax themselves, Levelt and Kelter (1982; also Schenkein, 1980) investigated syntactic persistence in a social context. In one of their experiments, the experimenter called various shops and either asked "What time does your shop close?" or "At what time does your shop close?". If the former question was asked, shopkeepers more often answered with "Five o'clock", whereas the answer to the latter question was "At five o'clock" in the majority of cases. Importantly, Levelt and Kelter (1982) as well as Schenkein (1980) obtained such effects of speech mimicry for single words, for clauses as well as for the structural format of entire sentences. Finally, Levelt and Kelter showed that cognitive load did not decrease these speech imitation effects, suggesting that these effects were automatic in nature.

1.1.4 Impacts of Behavioural mimicry

Examples in the last section remarkably demonstrate that mimicry behaviour is pervasive in our daily life. However, is this spontaneous mimicry just a funny tendency we (human) have and something we should leave to the realm of entertaining dinner conversation? Or is it an advanced behavioural

pattern that is critical to one's social survival? There is now strong evidence for the latter. Mimicry serves a critical function in our social interaction and social affiliation. In this section, I will review both the social and non-social impacts of mimicry.

Social Impacts of Mimicry

Liking and rapport within dyad. Early research on behavioural mimicry found a correlational relationship between mimicry and rapport. Charney (1966) examined postural congruence in the context of psychotherapy sessions and found that mimicry correlated with an increase in rapport between the therapist and client. LaFrance and Broadbent (1976) hypothesized that nonverbal behavioural mimicry could be a good index of group rapport. They assessed this hypothesis in college seminar classrooms and indeed found that students rated rapport as higher in classroom in which there was greater congruence between the body and arm positions of teachers and students. Other research also shows a strong link between mimicry and rapport. For example, a meta-analysis conducted by Tickle-Degnen and Rosenthal (1990) showed that the three facets of rapport—mutual attention, coordination, and positivity—are associated with particular nonverbal behaviours, with the coordination element of rapport being highly linked with mimicry.

Although these correlational data did not allow for the conclusion that mimicry leads to liking and rapport, several experimental studies did support this conclusion. Early studies by Maurer and Tindall (1983) suggested that adolescents who were mimicked by a school counsellor thought that counsellor was more empathic and likable than did those who were not

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mimicked by the counsellor. Chartrand and Bargh (1999, experiment 2) manipulated mimicry in the context of dyadic interactions to provide the first solid evidence that rapport is a consequence of mimicry. The dyad partners were complete strangers who presumably had no pre-existing rapport. One member of each dyad was a research confederate who was instructed to either mimic or not mimic the postures and mannerisms of the research participants while they completed a 'photo description task'. When questioned after the interaction, participants who were mimicked liked the confederate more and perceived their interactions as having run more smoothly than participants who were not mimicked. Hove and Risen (2009) have recently found similar effects for interpersonal synchrony. Specifically, they found that when one person synchronizes his or her movements in time with another, that other person (the mimickee) feels more affiliative (i.e. a positive and intimate feeling) with the synchronizer (mimicker). Bailenson and Yee (2005) even reported the rapport and affiliative effect of mimicry toward a virtual nonhuman, nonverbal mimicker. These findings provide firm evidence that mimicking the behaviours of interaction partners enhances rapport and facilitates social interaction.

Prosociality beyond dyad. The effect that mimicry leads to liking, affiliation and rapport between interaction partners suggests that it serves to bring people together emotionally. Does it also bring people together psychologically? Experimental research confirms this idea and suggests mimicry increases one's general prosocial orientation. Van Baaren et al. (2003a) conducted a study looking at tips given to waitresses in a restaurant. Waitresses were instructed to either recite back verbatim a customer's order

(verbal mimicry), or to paraphrase that order (indicating an understanding of the order without verbal mimicry). Tips given to the waitresses were used as the measure of prosociality. Results indicated that the waitresses received more substantial tips from customers whom they mimicked than from customers whom they did not mimic.

Mimicry increases one's prosociality not only within the dyad, but also towards the stranger they confront afterwards. In a study testing whether the rapport and affiliative feelings induced by mimicry would extend beyond the dyad, Ashton-James et al. (2007) found that participants who were mimicked on an earlier task reported on a questionnaire that they felt closer to others in general, compared to those participants who were not mimicked during the earlier task. In a second study, an implicit measure of feeling close to others was used—seating distance. Participants were either mimicked or not, and then asked to take a seat in a hallway where several chairs had been placed side by side. Several items were placed on one of the end chairs such that it looked like another participant was sitting there (but had stepped away). The implicit measure of feeling close to an unknown other was how close to the "occupied" chair the participant sat. The researchers found that participants who had earlier been mimicked sat closer to the occupied seat than participants who had not been mimicked. This suggests that mimicked participants were feeling closer to others, and again supports the notion that being mimicked increases one's general prosocial orientation.

In a study examining helping behaviour, participants were either mimicked or not by an experimenter (van Baaren et al., 2004). The experimenter then "accidentally" dropped a bunch of pens, and the amount of

pens picked up was the unobtrusive measure of helping behaviour. Participants who were mimicked picked up more pens for the experimenter than those who were not mimicked. In a follow-up study, researchers demonstrated that helping behaviour is not only limited to the mimicker. They found that mimicked participants also donated more generously to a charity than non-mimicked participants. Thus, individuals are more willing to help others after being mimicked than after not being mimicked. This effect was recently replicated with very young children (Carpenter et al., 2011). Eighteen-month olds were mimicked or not by an experimenter and subsequently observed the experimenter "accidentally" drop pens on the floor. The results revealed that mimicked children helped the experimenter pick up more pens than non-mimicked children.

It is not just the recipient of the mimicry (mimickee) who is influenced by mimicry—so does the mimicker. Stel et al. (2008a) have found evidence that mimicking others makes individuals more prosocial. Participants either mimicked the facial expressions of a person shown on a video or not. They were then asked to donate money to a charity, which was either related to the person on the video or unrelated. Consistent with results on mimickee, participants who were instructed to mimic (and who then in fact mimicked more) donated more to the charity (either related or unrelated) than those who did not mimic.

Nonsocial Impacts of Mimicry

Thus mimicry impacts individuals in a prosocial way, both within and beyond the mimicry dyad. It brings people together emotionally and cognitively. However, recently research suggests that mimicry also has non-

social impacts on interaction partners. Specifically, being mimicked or mimicking other can affect individuals' attitudes and creativity.

Attitudes. In consumer science, researchers found that when consumers are mimicked by a person, they show more positive attitude toward products presented by that person. In a series of studies by Tanner et al. (2008), a 'facilitator' told participants about a new snack product that was soon to be launched. The facilitator either mimicked the participants during the interaction or did not. After learning about the product and answering some questions about the product category, participants were asked to taste the product and rate how much they liked it, whether they planned to purchase it themselves and whether they would recommend it to friends. An index of favorability toward the product was computed from the responses to these questions. The results revealed that participants who had been mimicked by the facilitator had more favorable attitudes toward the product than those who had not been mimicked, although none of the participants attributed their attitude to the facilitator's behaviour. The authors argued that when consumers are mimicked, they feel more prosocial toward the mimicker, which in turn enhances the persuasion by the mimicker.

Creativity. There are two types of creativity: convergent creativity ("connecting the dots") and divergent creativity ("thinking outside the box"). Both are important skills that people use in their daily lives. Because mimicry brings people together and leads to a convergence in attitudes, Ashton-James and Chartrand (2008) hypothesized that mimicry would facilitate convergent creativity, whereas a lack of mimicry would facilitate divergent creativity. To test this theory, they manipulated whether individuals were subtly mimicked or

not by an experimenter during a five minutes social interaction, and subsequently measured participants' capacity for convergent thinking and divergent thinking. The results were just as predicted that the convergent creativity is significantly enhanced when being mimicked versus not being mimicked. They argued that being mimicked by an interaction partner cues convergent thinking by signaling a social opportunity for collaboration while not being mimicked cues divergent thinking by signaling a social demand for improvisation and innovation.

1.1.5 Social Modulators of Behavioural Mimicry

The Chameleon Effect (Chartrand and Bargh, 1999) did show that observing other's behaviour automatically activates one's tendency to copy that behaviour. However, subsequent research in social psychology revealed that we do not display the same extent of mimicry to everyone. Mimicry can be modulated by characteristics of the mimicker and mimickee.

Modulators from the Mimicker

Prosociality. Substantial evidence demonstrates that prosociality is a critical individual difference that modulates one's tendency to mimic. Long-term parameters of prosociality such as perspective-taking fundamentally gauge one's mimicry behaviour during social interation. For example, Chartrand and Bargh (1999, experiment 3) found that participants with high perspective-taking score mimicked the behaviour of a confederate to a greater extent than those with low perspective-taking score. Self-construal is another long-term index of prosociality that influences mimicry. Independent self-construal individuals tend to construe the self as separate from their social

context and thus emphasize autonomy and independence. In contrast, interdependent self-construal individuals tend to construe the self as a constituent of a broader social context and thus emphasize the interdepdendence and impact of social environment. van Baaren et al. (2003b) found that people with interdependent self-construals (e.g., Japanese) exhibited more unconscious mimicry than people with independent self-construals (e.g., Americans), regardless of the ethnicity of their confederate interaction partner.

Short-term characteristics of prosociality such as an affiliative goal also impact mimicry. Lakin and Chartrand (2003) found that having a goal to affiliate with others increases mimicry. In their experiment, they used two means to have participants with an affiliation goal, either by giving explicit instructions to require participants to get along with the confederate, or by implicitly priming participants with affiliation-related words such as affiliate, friend, partner, and together. They found that regardless of whether the affiliation goal was consciously instructed or unconsciously primed, mimicry is enhanced as long as one holds an affiliation goal. Leighton et al. (2010) found a similar effect of prosociality on mimicry. They exposed participants with scrambled sentences of prosocial attitude (e.g. 'Let us be together') or antisocial attitude (e.g. 'I am now single'). They found that participants primed with a prosoical attitude displayed more mimicry than ones primed with an antisocial attitude. These findings consistently suggest that temporarily increasing one's prosociality enhances one's tendency to mimic other.

Desire for belongingness. Another way to temporarily increase mimicry is to induce a desire for belongingness. As humans have a

fundamental and pervasive drive to affiliate with conspecifics (Baumeister and Leary, 1995; Lakin, et al., 2003), some studies suggest that inducing such need to belong to a group enhances mimicry. For example, Uldall et al. (2011) required students to complete a 'personality test' where some students were primed with a feeling of distinctiveness. Students were given a bogus feedback on the test which indicated they either had a common personality profile similar to most others or an extremely unusual one at their university. After they received the false feedback, they engaged in a task with a confederate who was shaking the foot throughout the interaction. Researchers found that those who had earlier been told that they were very different from others mimicked the confederate's foot shaking more than those who had been told they were similar to others. This suggests that people mimic more when they feel the need to belong to the majority.

Negative social experiences such as failure to affiliate with others or social ostracism can also induce a desire for belongingness and thus increase mimicry. For example, in the study by Lakin and Chartrand (2003), participants were asked to affiliate with a stranger in an online chat task. When researchers manipulated the stranger's response and made participants feel either a success or a failure in affiliating with the stranger, they found that those with a recent failure to affiliate with others showed more mimicry to others in a following social interaction. Similarly, in Lakin et al (2008), participants involved an online ball-tossing game called 'Cyberball' where ostracism was manipulated. Each participant played this online game with three other "participants" who were actually computer controlled to include or exclude the participant from the game. The results suggest that experiencing

ostracism does in fact increase participants' tendency to mimic others in a following social interaction. Similar effects of ostracism priming were later replicated in children (Over and Carpenter, 2009a).

Mood. It has been suggested that mood serves as a signal conveying information about the friendliness and dangerousness of our environment. A negative mood is assumed to indicate that something might be wrong and hence more self-focus attention and effortful analytic processes are adapted; in contrast, a positive mood is supposed to signal that the environment poses no threat, which leads to engage in more automatic and effortless stimuli-driven processes (Schwarz and Clore 1996). Based on the assumption that mimicry is an automatic process, it should become more easily engaged in a positive than in a negative mood. This prediction is in line with findings by van Baaren et al. (2006) who examined the effects of a happy and a sad mood on the mimicry of pen-playing. The authors found that individuals in a negative mood state hardly mimicked pen-playing, while individuals in a positive mood state did. Likowski et al. (2011) found similar effects on facial mimicry. They investigated whether a happy or sad mood influences facial muscular reactions to emotional facial expressions. Participants were induced into happy or sad mood states by watching an amusing or sorrowful movie. After that, they observed faces with happy, sad, angry and neutral expressions while their facial muscular reactions were recorded by EMG. Their results suggest that after watching the happy movie participants showed stronger facial mimicry to all emotional expressions, whereas watching the sad movie led to a general reduction of facial mimicry.

Modulators from the Mimickee

Likeability. Likeability is a key factor that influences how much a target would be mimicked. The more we like someone the more we mimic them (Stel et al., 2010a, 2010b). The likeability of a target, however, can be determined by many parameters. It can depend either on the most salient feature such as attractiveness or on the deep-rooted mindset such as stereotypes. Researchers have tested several parameters of likeability on mimicry. For example, van Leeuwen et al. (2009) found that when drawing a picture, participants are more prone to mimic the coloring mannerism of attractive people comparing to unattractive people. In contrast, Johnston (2002) provided the evidence that participants inhibit mimicry of the food consumption of the confederate if the confederate had a social stigma (being obesity, or having a facial scar).

Stel et al. (2010b) explored the relationship between mimicry and the stereotype of ethnic attitude. In their study, Dutch participants' ethnic attitude towards Moroccans was firstly measured by an 'implicit association test' (IAT, Greenwald et al. 1998). Participants then saw a video where a Moroccan or a Dutch person was talking and performing some subtle behaviour such as face/hair touching and pen-playing. They found that the more negative the participant's implicit attitude was toward Moroccans, the less Moroccans was mimicked compared to the Dutch confederate. This result means that when a mimicker holds a stereotype of dislike for a target, automatic mimicry is reduced.

Membership. Group membership is another feature that modulates mimicry. Several studies suggest that greater mimicry occurs to ingroup

members than outgroup members. For example, McHugo et al. (1991) demonstrated that facial mimicry to political leaders' photos was influenced by the observer's political membership. Supporters of Ronald Reagan showed more mimicry to his photos than towards his opponent's. This finding was later replicated by a well-controlled EMG study where the level of facial mimicry varies as a function of political membership (Bourgeois and Hess, 2008). Religion and ethnic membership can also impact mimicry (Chartrand and van Baaren, 2009). For example, Yabar et al. (2006) found that after identifying the religion belief of the targets, non-Christian participants displayed more mimicry towards non-Christian targets than Christian targets.

Social status. Most mimicry research to date examined situations in which people were of equal status (e.g. peers, friends). Only a few studies on mimicry included a manipulation of status by role. These studies suggested that people display more mimicry to higher status people than to lower status people (Brody and Stoneman, 1981; Cheng and Chartrand, 2003; Mastop et al., 2011). For example, in Cheng and Chartrand's study (2003), students were required to interact with a confederate in a role-playing task. Each student was randomly assigned to be a 'leader' or a 'worker' of the confederate (who took the opposite role). During the interaction, the confederate touched her face continuously. Results showed that those students who had been assigned the 'worker' mimicked the confederate's face touching much more than those who had been assigned to the 'leader' role, which suggests that lower status people tend to mimic more than people with high status. However, it is important to note that the increased mimicry to high status people is only limited to status-unrelated behaviour (e.g. face-touching,

pen-playing); for status-related behaviour (e.g. expanded posture), lower status people show increased complementary response instead of mimicry (Mastop et al., 2011).

1.1.6 Theories of Behavioural Mimicry

Previous sections reviewed the modulators and consequences of mimicry and suggested that mimicry can both impact and be impacted by multiple social factors. However, there is still a mystery for the purpose of mimicry—why people mimic each other. In social psychology, there are mainly two theories that address why people display overt mimicry behaviour.

Mimicry as an innate system

The 'nature and nurture' debate has already been taken in the research of mimicry. Here in social psychology, dominant theories seem to favor the nativist side (Meltzoff, 1993; Lakin et al., 2003; Chartrand and van Baaren, 2009). These theories are profoundly influenced by the longitudinal evidence of direct link between perception and behaviour in the evolution history (see the example of migrating fish and birds in 1.1.1) and the adaptive consequences that mimicry engenders (see 1.1.3). For example, Lakin et al. (2003) suggest that as mimicry has important survival value and social function, evolution selects mimicry as a social glue to help humans communicate and affiliate. Similarly, Meltzoff and Moore (1997) proposed that mimicry is a critical survival function which is acquired through natural selection and stored in the genome. They believed that humans are born with a tendency to mirror certain stimuli, or with foundational mechanisms that will support mimicry response after minimal environmental input. In particular, they

proposed that mimicry is based on an innate and specialized super-intermodal mechanism through which visual input from observed actions is matched to proprioceptive feedback from self-produced actions. This innate mechanism is important for infants' social learning and understanding.

The strongest support for nativist comes from the evidence that human/monkey neonates can mimic a range of facial gestures (Meltzoff and Moore, 1983; Ferrari et al., 2009). For example, Meltzoff and Moore (1977) showed that very young infants, even one infant of only 42 min, displayed facial mimicry (e.g. tongue protruding, mouth opening, pouting and sequential finger movements). These authors argued that if infants are able to mimic within hours or days of entering the world, their mimicry could not be based on learning; if they can mimic a range of behaviours, the innate endowment must be something more complex than a couple of reflexes. However, later meta-analysis of all the evidence in favor of neonate mimicry came to the conclusion that the only reliable mirroring effect across different studies and different laboratories is tongue protrusion (Anisfeld, 1996). Recent research even failed to find mimicry of tongue protrusion in infants (see a review from Jones, 2009). Jones (2006) described how other arousal stimuli increased the tongue protrusion response in very young infants, suggesting that tongue protrusion may not be an effect of mimicry per se, but an arousal response of oral exploration. Therefore, the weak evidence of neonate mimicry cannot support a nativist account of mimicry.

Finally, a strong formulation of nativist account is also incompatible with recent findings suggesting that mimicry is experience dependent, changing both with development (Perra and Gattis, 2008) and with relatively brief

training (Gillmeister, et al., 2008). I will present the evidence in a later section (see 1.2.5 and 1.2.6)

Mimicry as a Strategic Communication Tool

That mimicry behaviour occurs unconsciously does not preclude it from serving some higher functions. Nonverbal behaviour has long been thought to serve a communicative function (e.g., Scheflen, 1964). For instance, Kraut and Johnston (1979) found that people were more likely to smile in response to happy situations when there was another person around than when alone, which suggested that the smile served a communicative function. As a nonverbal behaviour, mimicry has also been thought of as a communication tool. Early theories suggest that mimicry is a way to ingratiate oneself to the other person (Piaget, 1946) and communicates understanding and togetherness between interaction partners (Bavelas et al., 1988; Bernieri, 1988; Condon and Ogston, 1966; Condon and Sander, 1974).

From an evolutionary perspective, it is not difficult to see that mimicry has adaptive communicative value. First, as mentioned in the beginning of this thesis, perception is the best guidance and control device of action (see 1.1.1). The perception of the behaviours by other members of our species communicate to us important features of the environment, such as the presence of predators, prey, and potential mates (Chartrand et al., 2005). If everyone is running away from a grizzly bear, it is not in one's best interest to find the bear, analyse the situation and determine that it is dangerous, and then run. Rather, upon seeing others run, running should come first, automatically and immediately, and then analysing the situation should come.

Therefore, coordination and mimicry have been argued to be necessary prerequisites for social survival (Condon and Sander, 1974; Kendon, 1970).

Second, recent studies suggest that mimicry is a strategic communication skill that helps people to get along with others. Group living has become the most influential factor in one's ability to survive and reproduce (Caporael and Brewer, 1991). Anthropology suggests individuals who were able to maintain successful harmonious relationships with others were at an evolutionary advantage (Caporael, 1997, 2001a, 2001b). Because mimicry enhances liking, affiliation and rapport between individuals (see 1.1.4), Lakin et al. (2003) proposed that mimicry acts as a communication tool to help people affiliate with others. They conducted two studies to test this idea.

First, Lakin and Chartrand (2003) examined whether people strategically increase mimicry when they have a goal to affiliate with others. Participants either had an unconscious affiliation goal, a conscious affiliation goal, or no goal while watching a "live feed of another participant in the next room" (actually a videotape of a confederate) who completed some tasks while continuously touching her face. The researchers found that having a goal to get along with someone, regardless of whether it was a conscious or a unconscious goal, led to an increase in mimicry (i.e., more face touching). In a second study, Lakin and Chartrand found that participants who had a goal to affiliate but failed to accomplish their goal were more likely to mimic another person in a subsequent task. This finding further demonstrates that people use mimicry as a strategy for affiliation (i.e., a means to an end), rather than simply an expressive display.

In another study, Lakin et al (2008) examined whether people

strategically increase mimicry when social relations collapse. Half of the participants experienced social ostracism by playing the 'Cyberball' game (see 1.1.6 for detail) while half did not. The results suggested that those who experienced ostracism showed more mimicry in a following social interaction than those who did not experience. Over and Carpenter (2009a) replicated this results in children and further suggested that the mere hint of ostracism enhances mimicry. In their study, children first watched a cartoon where a character was ostracized by others and then interacted with a human model. Results suggest that this third-party ostracism was sufficient to increase children's mimicry towards the human model. These findings suggest that people increase their mimicry when they sense a hint of disharmony, which supports mimicry as a strategy to keep oneself affiliated with others.

It is important to note here that the 'strategic nature' of mimicry means that people implement mimicry as an intervention to change the social world for self-advancement. It assumes that if I mimic Anna, she unconsciously detects the mimicry and changes her attitude towards me. Thus, I can use mimicry as a tool to make Anna like me, and will do this more if 'Anna liking me' is to my social advantage. From this point of view, the word 'strategic' no longer refers to any conscious decision-making process, but only describes that mimicry is driven by its affiliative consequence.

In summary, substantial evidence suggests that mimicry acts as a strategic communication tool. People increase mimicry when they want to affiliate with others (e.g. an affiliation goal) or they have to affiliate with others (e.g. social ostracism). This function has evolutionary roots because mimicry facilitates coordinate and affiliate in group living, which increases individuals'

survival rate. Therefore, it has been suggested that mimicry is like a weapon in people's unconscious arsenals, a tool in their behavioural repertoire used to keep successful relationships with others (Lakin et al., 2003).

1.1.7 Summary of Behavioural Mimicry Research in Social Psychology

Until now, we have reviewed the research of behavioural mimicry in social psychology. Past research used naturalistic paradigms to investigate what, how and why people mimic. Specifically, a large battery of studies demonstrated that people unconsciously copy the body movements, facial expressions, speech style of the interaction partner and this behavioural mimicry is grounded on a primitive close link between perception and behaviour. Research on the consequences and modulators of behavioural mimicry suggests that mimicry has positive social impacts on both mimickers and mimickers. It enhances liking and rapport between interaction partners and increases mimickee's general prosocial orientation. Although behavioural mimicry is spontaneous and unconscious, it is sensitive to social contexts and can be modulated by a series of characteristics from the mimicker (e.g. prosociality, belongingness and mood) and the mimickee (e.g. likeability, membership and social status) (Figure 1-1). Theories of why people mimic suggest that mimicry functions as a strategic communicative tool to maintain a successful interpersonal relationship with others.

Modulators of Mimicker
-Prosociality
-Belongingness
-Mood

Rapport within a mimicry dyad

Modulators of Mimickee
-Likeability
-Membership
-Social status

Mimicry

General prosocial orientation

Cognitive influence on the individual such as attitude and creativity
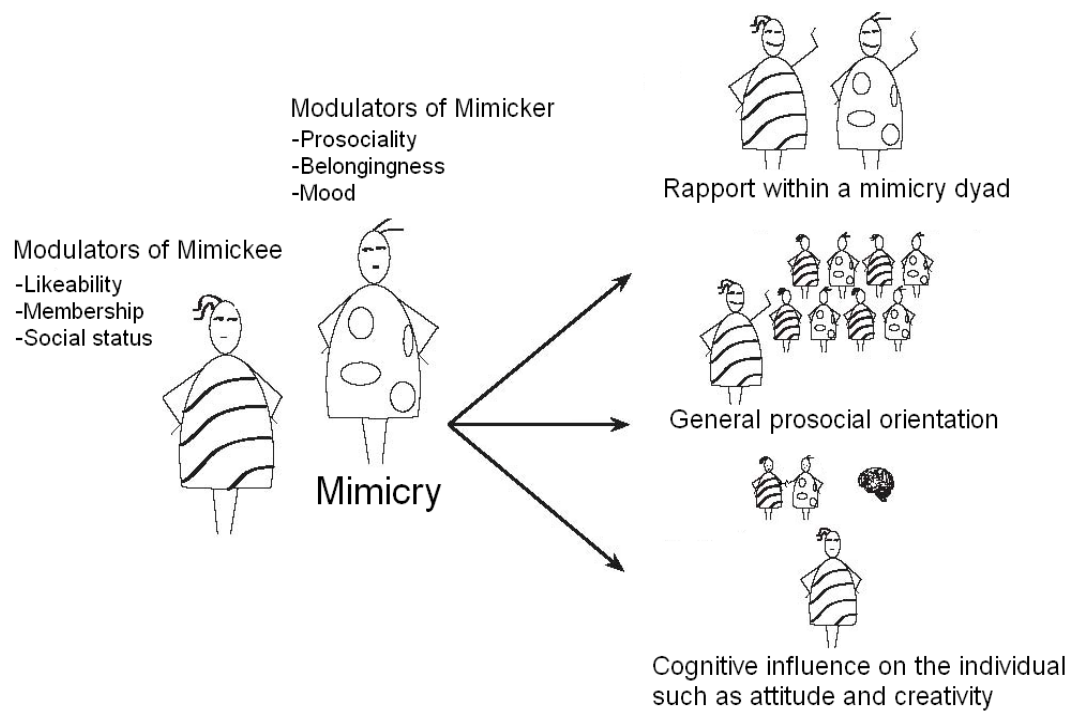
Figure 1-1. The consequences and modulators of behavioural mimicry (modified from Chartrand and van Baaren, 2009)

1.2 Mimicry in Cognitive Neuroscience

Different from above-mentioned studies in social psychology that focuses on the visible mimicry behaviour during interactions, research in cognitive neuroscience primarily investigate the underlying mechanism of mimicry. This perspective can date back to Descartes' time where scientists and philosophers debated on the origin of action (Descartes, 1664). Also, William James discussed about the relationship between perception and action and claimed that 'every mental representation of a movement awakens to some degree that actual movement which is its object' (James, 1890). In contemporary cognitive neuroscience, researchers use a series of cognitive-behavioural, neurophysiological and neuroimaging techniques to study mimicry, thus a variety of names have been given to describe one's tendency to mimic, including 'motor priming' (Liepelt et al., 2008), 'social mirroring' (Iacoboni, 2005) and 'automatic imitation'(Heyes, 2011). In this thesis, I will use a more general term 'mimicry effect' to describe this tendency.

Here in the second half of the introduction chapter, I will present an overview of studies that investigated the mechanism of mimicry in cognitive neuroscience. I will first introduce the findings that point to a tight interplay of perception and action (see 1.2.2) and the evidence that supports the existence of mimicry effect (see 1.2.3). Then I will provide findings showing that mimicry has impacts to other cognitive functions (see 1.2.4) and it can be flexibly modulated by other cognitive factors (see 1.2.5). Finally, I will outline theories and empirical studies which address how the mimicry effect happens in the cognitive and neural level.

1.2.1 Methodologies

Different from studies in social psychology where researchers use natural paradigms to investigate human social behaviour, cognitive psychologists use several simple but reaction-time based stimulus-response compatibility (SRC) paradigms to investigate action and perception. In most SRC paradigms, action comes about as re-actions to certain stimuli, and they do so by virtue of assignment rules as fixed in the experimental instructions. For example, in the famous 'Simon effect' task, participants are instructed to respond to a green object by pressing a left key and to a red object by pressing a right key. In each trial, the objects would be randomized presented either at the left side or the right side of the screen. Results suggest a substantial spatial compatibility effect between action and perception, where responses are usually faster and more accurate when the stimulus occurs in the same relative location as the response (e.g. green object presented on the left side), even if the stimulus location is irrelevant to the task (Simon 1990; Hommel and Prinz, 1997).

Two special types of stimulus-response compatibility (SRC) paradigm have been widely used to measure mimicry in cognitive neuroscience: action selection paradigm (e.g. the 'finger tapping task') (Brass et al., 2000, 2005; Bertenthal et al., 2006) and action initiation paradigm (e.g. the 'hand opening/closing task') (Heyes et al., 2005; Press et al., 2008) (see 1.2.3). Different from the 'Simon effect' task where compatibility is based on spatial location, these two paradigms use action congruency as the compatibility dimension: they set photos or videos of hand/finger movements as stimuli and require participants to perform congruent/incongruent movement as response. For example, in the 'finger tapping task' where action selection paradigm was

adopted (Brass et al. 2000) (Figure 1-2), participants were instructed to select a finger to press in response to a cue appeared in a box (+: index finger, x: middle finger) while viewing incongruent or congruent finger movements around the box. In congruent trials, the hand in the video frame executed an identical finger movement to the selected movement (e.g. '+' appeared while the index finger was moving in the video), while in incongruent trials the movement executed by the hand on the screen was different from the selected movement (e.g. 'X' appeared while the index finger was moving in the video) (Figure 1-2). In baseline trials, the hand on the screen did not perform any hand movement, left only the cue appearing. Participants were asked to respond to the cue as quickly as possible and to disregard the moving finger in the background. Because in congruent trials participants were facilitated by the mimicry of observed action and in incongruent trials participants had to enforce the intended action against the mimicry of observed action, mimicry is measured by calculating the reaction time difference between congruent trials and incongruent trials (Brass et al., 2000)
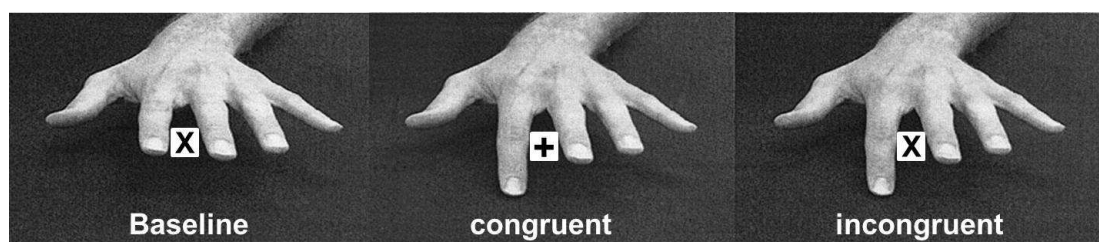
Figure 1-2. Illustration of the 'Finger tapping task' used by Brass et al. (2000). In each trial, participants have to press a button by using either index finger or middle finger in response to a symbolic cue (+ : index; X: middle), while observing a congruent or incongruent finger movements around the symbolic cue.

The action initiation paradigm adopts a similar way to measure mimicry, but pre-specifies the response of each block. In the 'hand opening/closing task' created by Heyes et al. (2005) (Figure 1-3), participants were required to make the same pre-specified response (to open or close their right hand) in every trial of a block, as quickly as possible after the hand in video clips began to move. On some trials, the stimulus hand opened and on others it closed. Therefore, within a block, the hand movement stimulus was either the same as the pre-specified response (congruent trials, e.g. close stimulus and close response) or the opposite of the pre-specified response (incongruent trials, e.g. open stimulus and close response) (Figure 1-3). Participants' response movement direction was orthogonal to stimulus movement direction (to avoid spatial compatibility confounds, see why in 1.2.3) and were instructed to respond as quickly as possible in all trials.). Again, mimicry is measured by calculating the reaction time difference between congruent trials and incongruent trials (Heyes et al., 2005).

Five pairs of action types other than index/middle finger tapping and hand opening/closing have also been used in these two paradigms: power/precision grip (Chong et al., 2009), index finger lifting/tapping (Brass et al., 2001a), index/little finger abduction (Catmur and Heyes, 2011), mouth opening/closing (Leighton and Heyes, 2010), hand/mouth movement (Leighton and Heyes, 2010). In the experimental chapters of this thesis, we adopted the 'finger tapping task' and 'hand opening/closing task' to measure mimicry.
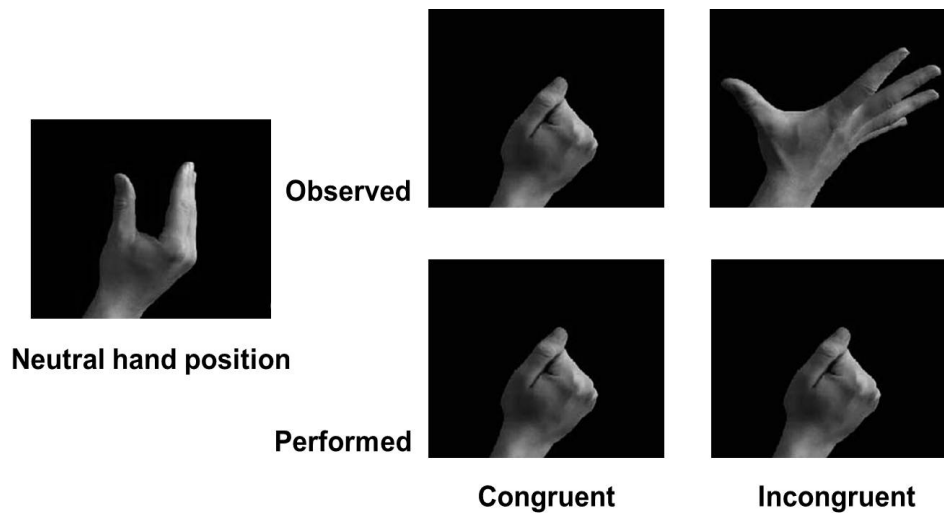
Figure 1-3. Illustration of the 'hand opening/closing task' used by Heyes et al. (2005). In the beginning of each trial, participants have to keep a neutral hand position. As soon as the hand in the video starts to move, participants are required to perform a pre-specified hand movement (hand open or hand close) as quickly as possible. The pre-specified reponse could either be congruent or incongruent with the observed action.

1.2.2 Perception-Action Link

For a long time, perception and action have been considered as separated and peripheral processes. For example, influenced by the developments in the computer sciences of the 1950s, traditional approaches within the field of cognitive science views the mind as an analogy of computer, which is a symbol manipulator. It usually has three units: perception, cognition and action. Perception involves the translation of physical stimuli into symbolic representations. Once stimuli are perceived, cognition unit can integrate and analyze them for decision-making or store them in memory as symbolic codes. If the decision involves physical response, then these symbolic codes would be passed on to the motor system for action generation. Therefore, perception

and action are two isolated processes and action execution is merely one option of cognition. Perception and cognition drive action, but action does not influence perception and cognition.

Recent developments cast doubt on the feasibility of this approach as a general framework for understanding human mind. Substantial evidence in cognitive psychology suggests that perception and action are inseparable. Here I will review two lines of research supporting this close link: first, action planning and control can modulate perception ('action modulates perception'); second, mere perception of an action would affect the way in which an observer plans or executes actions which resemble the observed action ('perception modulates action').

Action modulates perception

Blindness effect for response compatible stimuli. Musseler and colleagues conducted several studies where they explicitly addressed the question of whether planning an action modulates the concurrent perception of events in the environment (Musseler and Hommel, 1997; Musseler et al., 2000). In their studies, participants were first presented an arrow cue (arrow 1) indicating which key they had to press (e.g. when seeing a left pointing arrow they had to press a left key and when seeing a right pointing arrow they had to press a right key). However, instead of immediately executing the left or right key press, they had to press both the left and right key simultaneously (double key press) to initiate the response time recording. The double key press would immediately initiate a presentation of a left or right pointing arrow (arrow 2), which was masked immediately afterwards. The participants' task was first to carry out the key press they had planned in advance (in response to arrow 1)

as fast as possible, and then to identify the direction of the arrow 2 as accurately as possible (without time pressure). Results showed that the identification rates for the arrow 2 were lower when the planned action (arrow 1) and the masked stimulus (arrow 2) were the same direction. For example, arrows pointing to the right were often less correctly identified while planning a right action than while planning a left action. The authors suggest that this disadvantage is due to the fact that event representations that are currently needed in order to plan an action are shielded from further perceptual input (Musseler et al., 2000).

Weight judgement. Hamilton et al. (2004) investigated whether actually performing an action influences the concurrent perception of an observed action. Participants were asked to judge the weight of a box lifted by an actor while either lifting or passively holding a light or heavy box. They found that holding a box systematically biases observers' judgments of the weight of a box lifted by another person. For example, if an observer holds a light box while judging the weight of a box lifted by another person, the observer judges the other's box to be heavier, and vice versa when the observer holds a heavy box. Similar to Musseler et al (2000)'s explanation for the blindness effect for response compatible stimuli, the authors interpreted the results in terms of a functional overlap between perception and action systems where this overlap could not contribute to both the action task and perceptual task simultaneously, so participants who are lifting a heavy box will shield from a judgment of heavy weight and participants who are lifting a light box will shield from a judgment of light weight.

Ambiguous motion display. Wohlschlager (2000) conducted a study

that convincingly demonstrates that action modulates perception. In his experiments, participants observed an ambiguous motion display. The display consisted of a number of disks in a circular arrangement which were shifted by a constant angle about 6 times/s. When this display is observed under neutral conditions, one would get an impression that the disks could move either in a clockwise or a counterclockwise manner. In other words, the movement direction experienced in the display is ambiguous. In the first experiment, Wohlschlager instructed participants to rotate a knob clockwise or counterclockwise in the same plane as the motion display. The motion display came on as soon as they started their movement. As expected, the movement direction clearly affected the perceived direction of the ambiguous motion. For example, when the participants rotated the knob in a clockwise direction, the ambiguous motion display was more often perceived as rotating clockwise.

A following experiment further demonstrates that it is not necessary actually to execute a movement to obtain such effects. Participants were asked to either plan a clockwise or counterclockwise movement before the ambiguous motion display came on and to carry out the movement only after reporting the perceived direction of the ambiguous motion. The results were basically the same as for the experiment in which the participants concurrently carried out a movement. For example, when they planned a clockwise movement they were more likely to perceive a clockwise movement in the ambiguous motion display. These results provide clear support for the claim that action and perception are inseparable.

Perception modulates action

Action induction. Action induction refers to the phenomenon that the

mere observation of others' actions can spontaneously induce actions on the part of the observer. It is often referred in the literature as 'ideomotor movements' (Prinz, 1987). For example, when watching an actor in a film who walks along the edge of a plunging precipice, people are often unable to sit still and watch quietly. They will move their legs and their arms or displace their body weight from one side to the other.

Action induction used to be understood as a result of mimicry: when the actor bends toward a precipice on the right, people in the audience would also incline to bends toward right (Carpenter 1874; James, 1890). However, recent studies suggest that action induction results from intentional induction (Knuf et al. 2001; de Maeght and Prinz, 2004). They claimed that people realize (or fulfill) what they would like to see happening in the scene through their induced movements. Therefore, in the film example they would predict that when the actor bends towards a precipice on the right, people in the audience should bend to the left (to avoid falling down). Although it is still controversial whether action induction is based on a mimicry or an intentional assumption, the phenomenon per se suggests that perception can profoundly influence the observer's action.

Interference by human movements. Kilner and his colleagues (2003) conducted a study where they found a strong interference effect of observed human movements on action. Participants made vertical or horizontal sinusoidal movements with their right arm while observing either a robot or an actor making congruent (same direction) or incongruent (tangential direction) sinusoidal arm movements. Variance in the executed movement was measured as an index of interference to the movement. The results

demonstrate a significant interference effect on executed movements when observing an actor making incongruent movements, whereas no such interference effect occurred when subjects observed a robotic arm making incongruent movements. These results suggest that observing an action made by a human, but not by a robot, interferes with executed actions.

1.2.3 Evidence of Mimicry Effect

The last section reviewed studies suggesting that action and perception are intrinsically linked. However, the direct evidence of mimicry effect comes from two special biological effects—Fadiga's effect in motor evoked potentials (MEPs) and Congruency Effect (CE) in action initiation and selection.

Fadiga's effect in MEPs

The first demonstration of mimicry effect comes from the "mirror" MEPs elicited during action observation by Fadiga and his colleagues (1995; Strafella and Paus, 2000). They applied transcranial magnetic stimulation (TMS) to the primary motor cortex during passive action observation and found that the amplitude of the MEPs, as evoked by TMS, was specifically and significantly modulated by the observed actions. The MEPs recorded from the muscles required to execute that action is greater than the amplitude of the MEPs recorded from task-irrelevant muscles. For example, observing handwriting and arm movement stimuli selectively facilitated the amplitude of MEPs recorded from the first dorsal interosseus (responsible for handwriting movements) and biceps brachii (responsible for arm movements), respectively (Strafella and Paus, 2000). Therefore, the Fadiga's effect suggests that the passive observation of actions may activate associated motor representations.

CE in action selection and initiation

Sturmer et al. (2000) is one of the earliest studies to investigate whether selecting a simple hand movement is affected by the concurrent perception of a related finger action. In their study, participants observed one of two hand movements after a neutral starting posture hand been displayed: either the fingers were extended to spread the hand apart or the fingers were flexed to form a grasping movement. With the onset of the movement a color cue was superimposed on the hand observed. Participants were instructed to perform a spreading action or a grasping action with their right hand in response to the color cue. For instance, they performed the spreading action when the color cue was red and the grasping action when the color cue was blue. Thus the hand action observed was completely irrelevant for selecting the action to be performed. Nevertheless, the authors observed substantial CE between the observed irrelevant hand action and the hand action to be performed. For example, when participants were instructed to perform a spreading action in response to a red color cue, they selected the action faster when the observed hand also performed a spreading action. This CE on action selection was later replicated in the finger tapping tasks by Brass et al (2000) (see 1.2.1).

Brass et al. (2001b) investigated whether initiating a simple finger action is affected by the concurrent perception of a related finger action. They adopted an action initiation paradigm similar to the 'hand opening/closing task' (see 1.2.1), but used index finger lifting/tapping as action type. In each trial of their study, participants observed one of two stimulus sequences in random order. Both started with a static picture of a hand where the index finger was

at the center. After a variable and therefore unpredictable amount of time, the finger started moving upward in one sequence or downward in the other sequence. Participants were instructed to move their own index finger either upward or downward as soon as the observed finger started moving. Importantly, during a given block of trials the movement conducted by the participant remained the same. In other words, participants would see a randomized sequence of up and down movements of an index finger, but they always carried out the same action (e.g. moved their index finger downward). Accordingly, the action to be performed was pre-specified throughout, and the identity of the triggering stimulus (moving up versus down) was completely irrelevant. The question was whether the irrelevant stimulus gesture would still affect the time needed to initiate the action.

The results demonstrated that it took the participants longer to initiate a simple action when the observed action had a different direction than the observed one had the same direction. For example, upward movements were initiated slower when triggered by downward-moving stimulus gestures, and downward movements were initiated slower when triggered by upward-moving stimuli. This pattern of results was in nature different from the CE on 'Simon effect' task or the effect on action selection tasks I just discussed, because participants in those tasks need to select between two different actions. Hence the most surprising aspect of the study by Brass et al., (2001b) is that a CE was observed for a simple and completely pre-specified action. These results provide strong evidence of the existence of mimicry effect that contributes to the CE; otherwise, the time it takes to initiate a simple action should not be affected by the action observed.

The CE on action initiation and selection has been reported in several many effector systems, including finger movements (Brass et al., 2000, 2001b; Catmur et al., 2007; Catmur and Heyes, 2011), whole hand gestures (Sturmer et al. 2000; Heyes et al, 2005), mouth movements (Leighton and Heyes, 2010), and facial expressions (Dimberg et al, 2002). The effects happen to both transitive (object-directed) actions (e.g., Brass et al., 2001a) and intransitive actions (e.g., Press et al, 2008) and can be dissociated from the spatial compatibility seen on 'Simon effect' task. For example, a recent review by Heyes (2011) presented seven mimicry studies where left-right, up-down, and/or orthogonal spatial compatibility have been controlled. These studies provided clear evidence that the CE on action initiation and selection are mainly contributed by mimicry effect, but not solely to spatial compatibility.

1.2.4 Impacts of Mimicry Effect on other Cognition

Mimicry effect has been suggested as a reflection of 'embodied simulation' (Gallese, 2009). It claims that mimicry directly bridges other's behaviour with one's own and facilitates the understanding of perceived behaviour. Researcher have attempted to link mimicry to a wide variety of social functions, such as action understanding, theory of mind, empathy and language comprehension; however sparse evidence has been found. Here I will only review some solid evidence of the impacts of mimicry effect in emotion recognition and person perception.

Emotion Recognition. Traditional embodied cognition theory suggests that mimicry contributes to the recognition of affect experienced by others (Barsalou et al., 2003; Niedenthal, 2007; Niedenthal et al., 2010;

Gallese, 2009). Specifically, by mimicking another's emotional expression, one experiences the corresponding emotions him-or herself (i.e., experiences empathy), which in turn facilitates instantaneous emotion recognition. Oberman et al. (2007) and Stel and van Knippenberg (2008) used a similar paradigm to test this idea. Participants in their studies were asked to indicate quickly and accurately whether briefly displayed facial emotions were positive or negative. The emotions were shown on a computer screen for a short (but not subliminal) amount of time. While doing this task, half of the participants had facial constraints (e.g. clench teeth) that prevented them from engaging in natural mimicry. Results revealed that when participants were constrained and could not mimic, the speed of their recognition of affective valence was slowed down. These studies suggest that mimicry plays an important role in understanding the emotions of others; it facilitates the speed of affect recognition.

Person Perception. Coordinated behaviours are essential components of social interaction. Macrae et al., (2008) hypothesized that this synchronization of movements during a dyadic interaction may prompt increased attention to be directed to an interaction partner, hence facilitate the cognitive process of person perception. To test this, they asked participants to make hand movements (hand-up-hand-down) in response to the beat of a metronome. Participants were told that they should only concentrate on moving in time with the metronome and ignore any distractions from the experimenter where the experiment would either synchronized her right hand movements with those of the participant (i.e., participant hand-up, experimenter hand-up) or de-synchronized the movements (i.e., participant

hand-up, experimenter hand-down). The experimenter would also utter a series of potentially distracting words during the hand movements. When the task was over, the experimenter left the room and participants were tested on some incidental memories of the previous experimenter's behaviour. The results showed that when the experimenter provided synchronized movements with the participant, participants demonstrated enhanced memory for the experimenter's utterances and facial appearance. This suggests that synchronized behaviour enhances the acquisition of person knowledge.

1.2.5 Cognitive Modulators of Mimicry Effect

As a direct link between action and perception, mimicry is vulnerable to factors that can affect either perceptual processes or motor processes. These factors include arousal, attention, animacy and sensorimotor experience.

Arousal. Fujimura et al. (2010) investigated the effect of facial expression arousal level on facial mimicry. High- and low-arousal facial expressions indicating pleasant and unpleasant emotions were presented to participants where their facial electromyographic (EMG) reactions were recorded from the zyogmatic major (key muscle for pleasant expression) and corrugators supercilii muscles (key muscle for unpleasant expression). Results showed that stronger zygomatic major muscle activity was evoked for high- compared to low-arousal pleasant expressions; but for unpleasant expression, comparable activity was induced in the corrugators supercilii muscle in response to both high- and low-arousal level. These results suggest that the arousal levels of pleasant, but not unpleasant, facial expressions can enhance facial mimicry.

Attention. Early research suggests that natural imitation behaviour can be induced by joint attention in monkeys (Kumashiro et al., 2003, 2008). Chong et al. (2009) examined the effect of selective attention on mimicry. In their experiment, participants were presented with go/no go stimuli consisting of a color cue (red or blue) or a hand movement cue (a power or precision grip). They had to perform a hand movement (a power or precision grip) as soon as they saw the cue. There was a congruent effect when participants were instructed to use stimulus grip as the go-no go signal, simply because participants mimic the observed congruent/incongruent movement. However, when participants were instructed to use color cue as the go/no signal, the congruency effect disappeared. This finding demonstrates the importance of selective mechanism in the limiting the mimicry of irrelevant observed actions.

Animacy. Several studies suggested that mimicry can be modulated by high-level cognitive processes, such as the animacy of a movement (Liepelt and Brass, 2010; Longo and Bertenthal, 2009; Longo et al., 2008; Press et al., 2007). They claimed that mimicry has a biological bias toward the perception of intentional agents and pointing one's attention to the animacy of a movement (whether the movement is performed by human or the movement is 'artificial', 'robotic', 'biomechanically impossible') can modulate the mimicry of that movement. For example, Press et al. (2007) found that compared to robotic action stimuli (both natural and schematic), participants have a stronger mimicry effect to human action stimuli. Longo et al. (2008) tested the mimicry of observed finger actions while manipulating whether the movements were biomechanically possible or impossible. When no mention was made of this difference, comparable mimicry was induced from both possible and

impossible actions. When attention was drawn to the difference of animacy, however, only possible movements induced the mimicry effects. Similarly, Longo and Bertenthal (2009) displayed both photographic and computer-generated hand stimuli to each participant and instructed that some of the stimuli were computer-generated. They found that the magnitude of mimicry induced by the computer-generated stimuli was much smaller than by the photographic stimuli; it was also smaller than the mimicry observed in another group of participants who only saw computer-generated stimuli and were never told about their origins.

Other animacy studies have shown that, even identical natural human movement stimuli was presented, participants' beliefs about the origin of those stimuli or the efforts to execute the stimuli can modulate mimicry. For example, Liepelt and Brass (2010) tested the magnitude of mimicry induced by finger movements of a hand in a leather glove. Before running the experiment, they presented either a human hand or a wooden analog hand wearing the leather glove. They found that the group that believed the finger movement was generated by a wooden hand showed a smaller magnitude of mimicry than the group that believed they were observing human movements. In another study examining beliefs about the efforts involved in making stimulus movements, Liepelt et al. (2008) presented finger movements either inside an open or a closed metal clamp. The design of finger movements in a closed metal clamp aimed to give the impression that the hand tries hard to do the finger movement against the clamp. Although only tiny movements were visible in both conditions, they found a larger mimicry effect when finger movements were presented inside a closed metal clamp. They argued that

this finding, along with previous animacy studies, suggests that mimicry can be top-down modulated by intentional attribution.

Sensorimotor Experience. Empiricist theories (see 1.1.6) have a strong claim that mimicry comes from sensorimotor learning. Several studies using a stimulus-response compatibility paradigm support this claim and showed that sensorimotor experience can enhance, abolish and even reverse mimicry. For example, Press et al.(2007) found the classic animacy effect on mimicry in a pre-test where participants showed stronger mimicry to human action stimuli than robotic action stimuli. However, twenty-four hours after a relatively brief period of congruent sensorimotor training with the robotic action stimuli—where participants responded to robot hand-opening stimuli by opening their hands and to robot hand-closing stimuli by closing their hands— the animacy bias in the pre-test was abolished and the robotic action stimuli elicited as much mimicry as the human action stimuli. In a complementary way, Heyes et al. (2005) showed that incongruent sensorimotor training with human stimuli—in which participants responded to human hand opening by closing their hands and to human hand closing by opening their hands— abolished mimicry effects. Twenty-four hours after training of this kind, responding in incongruent trials was as fast as responding in congruent trials. Similarly, Catmur et al. (2007) showed that, in the case of little- and index-finger abduction movements, incompatible sensorimotor experience can reverse mimicry effects, producing a systematic, involuntary tendency to counter-mimic the observed action.

It important to note that in all of the above-mentioned training studies, participants were exposed to and executed each stimulus action (e.g. hand

open/close) equally often during congruent (e.g. open stimulus—open response) and incongruent (e.g. open stimulus—close response) training. The fact that only incongruent training abolished or reversed mimicry effects provides the solid evidence that it is the sensorimotor experience—not sensory experience or motor experience—that modulates mimicry.

1.2.6 Theories of Mimicry Effect

Although mimicry has been investigated for decades, the underlying mechanism is still poorly understood. In this section, I will review five popular theories of mimicry effect in cognitive neuroscience. Although these theories are grounded on different empirical evidence from behavioural, neurophysiological and neuroimaging studies, they all aim to address how information is processed in the brain during mimicry.

Sensorimotor theory

The first framework is 'sensorimotor theory', which can be traced back to Descartes' analysis of the relationship between action and perception (Descartes, 1664). Basically, this theory proposed that human actions must be understood as responses to the external stimulation. In other words, it treats actions as re-actions, that is, as responses triggered by stimuli. For example, Gibson proposed a notion of "affordances" where the environment stimuli directly suggest the appropriate behavioural response to them – the grilled lobster says "eat me" and the cold glass of beer says "drink me" (Gibson, 1979; McArthur and Baron, 1983). In sensorimoter framework, action and perception have independent representational formats: perceptual representations code patterns of stimulations in the sense organs and certain

properties that are derived from these patterns whereas action representations represent patterns of excitations in muscles or certain regularities occurring in these patterns. External stimuli must be translated into motor responses by arbitrary stimulus -response mapping mechanisms, or called S-R bonds (e.g. Skinner, 1938; Watson, 1913).

The sensorimotor perspectives on action and perception used to be predominant in both modern physiology and cognitive sciences. It helped to found a number of experimental methodologies such as reaction time measurement (Helmholtz, 1852; Donders, 1862) and behaviourist programme (Watson, 1913; Hull, 1943). However, this perspective has several limitations. First, it cannot explain the process of voluntary actions where the external stimuli can be reduced into its least form (Lotze, 1852). Second, these "affordance "responses to stimuli are not imitations of the perceived event but are stamped in as a habit based on one's past reinforcement history. Third, the sensorimotor framework introduces another fundamental question to mimicry, known as 'correspondence problem': how is the sensory input from somebody else's action transformed into a matching motor output by the mimicker (Brass and Heyes, 2005; Nehaniv and Dautenhahn 2002)?

Ideomotor theory

The second view on action is 'ideomotor theory', which mainly postulates that actions are caused by intentions (Greenwald, 1970, 1972). Its origin can date back to William Carpenter and William James more than hundred years ago with the argument that thinking about an action is sufficient to lead to the performance of that action (Carpenter, 1874; James, 1890; Wegner, 2002). Unlike sensorimotor views, ideomotor views stress the role of internal

(volitional) causes of action and disregard the role of external (sensory) causes. On this view, actions are considered creations of the will—events that come into being by virtue of the fact that people pursue goals and entertain intentions to realize them. The evidence on which ideomotor theories are grounded does not come from stimulus-constrained reaction tasks but rather from more open situations where individuals pursue certain goals and from time to time, perform certain actions in an attempt to approach, or achieve them, such as action induction (Prinz, 1990, 1997, Hommel et al., 2001; see 1.2.2).

The core assumption of ideomotor theory could be called the goal-trigger hypothesis. It holds that goal representations, which are perceptual anticipations of action effects, play a crucial role in action control. Actions are represented neither in terms of stimuli nor responses but in terms of the perceptual consequences. This point of view significantly advances people's understanding of action and perception and provides an attractive answer to the question of how voluntary actions are prompted and guided through internally generated anticipations of the perceptual consequences of an action. However, the traditional ideomotor theory emphasizes too much on the internal, voluntary part of actions but neglects the influences from the external environment. It sets up the link between cognition (goal or planning) and action, but not exactly the link between perception and action. It also has limitations in explaining how human unconscious and spontaneous behaviour comes about.

Common coding theory

As mentioned above, the sensorimotor theory stresses the crucial role of

perception on action and the ideomotor theory elaborates how actions are represented and prompted by goals. However, neither of them can fully explain the relationship between action and perception and the mechanism of mimicry. Recently, Prinz (1990, 1997, 2002, 2005a, b) proposed a 'common coding theory', which assumes a common representational format for perception and action. This is a novel framework that blends elements from the sensorimotor and the ideomotor stance. Specifically, it suggests that on top of separate coding for action and perception, there are domains of representation in which afferent and efferent information share the same format and dimensionality of representation, and this shared representation is the perceptual consequences of that action. As long as the perceptual consequence is accessed, both the afferent and efferent part of the action can be influenced. Such a claim suggests that observed and executed actions are represented in a commensurate manner: seeing an event activates the action associated with that event, and performing an action activates the associated perceptual event. It also permits interference effects when action and perception attempt to access the shared representations simultaneously. Moreover, this claim predicts that action and perception can reciprocally modulate each other: action planning and control can modulate perception and perception can modulate action planning and control. These three predictions have been supported by multiple studies (Knoblich and Prinz, 2005)

The common coding framework fundamentally solves the corresponding problem of mimicry and makes translational processes between stimuli and responses rather unnecessary. Since action and perception are commonly

and commensurately represented, perceiving other's movements automatically activates the corresponding motor representations of one's own. It makes the process of mimicry a very simple story: perceiving is for doing. However, where is the neural substrate of this shared representation in the brain? The discovery of the mirror neurons tackles with this question.

Mirror Neuron theory

The remarkable discovery of mirror neurons in monkeys supports the common coding theory and provides the first direct evidence that action observation and action execution are commonly coded at the same neural level. Mirror neurons are visuomotor neurons that fire both when an action is performed, and when a similar or identical action is passively observed (Rizzolatti and Craighero, 2004). Mirror neurons were first identified using microelectrode recordings of single neurons in area F5 of the monkey premotor cortex (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996) and later also in the PF/PFG complex within the inferior parietal cortex (Gallese et al., 2002; Fogassi et al., 1998; Fogassi and Luppino, 2005). The function of mirror neurons in monkeys is believed to mediate the action understanding (Rizzolatti and Craighero, 2004). For example, a mirror neuron which fires when the monkey rips a piece of paper would also fire when the monkey sees a person rip paper, or hears paper ripping (auditory cues) (Keysers et al. 2003). These properties have led researchers to believe that mirror neurons encode abstract concepts of actions like 'ripping paper', whether the action is performed by the observer itself or other monkeys.

It is not normally possible to study single neurons in the human brain, so most evidence for mirror neurons in humans is indirect (see an exception of a

recent single-neuron recording study by Mukamel et al., 2010). Brain imaging experiments using functional magnetic resonance imaging (fMRI) have shown that the human inferior frontal gyrus (IFG) and superior parietal lobe is active when the person performs an action and also when the person sees another individual performing an action. Because these two regions are homologue of monkey area F5 and PF/PFG in anatomy, they are believed to contain mirror neurons and defined as the human mirror neuron system (MNS) (Rizzolatti and Craighero, 2004). However, more recent experiments have shown that the regions with mirroring property are present in various cortical areas, including superior temporal sulcus, human Broca's area, supplementary motor areas, primary somatosensory cortex, insula and anterior cingulate cortex (Rizzolatti and Fabbri-Destro, 2008).

The function of the human MNS is a subject of much speculation. Many researchers consider that this system may be important for understanding the actions of other people, and for learning new skills by imitation (Rizzolatti and Craighero, 2004). Some researchers also speculate that mirror systems may simulate observed actions, and thus contribute to theory of mind skills (Gallese and Goldman, 1998) while others relate mirror neurons to language abilities (Rizzolatti and Arbib, 1998). It has also been proposed that problems with the mirror system may underlie social function disorders, particularly autism (Iacoboni and Dapretto, 2006; Ramachandran and Oberman, 2006; Williams, et al., 2001). However, except for action understanding and imitation (Rizzolatti and Craighero, 2004), the connections between MNS and other social functions are tentative.

The discovery of mirror neurons not only provides a physiological

mechanism that action observation and action execution are coded at the same neural level, but also support other claims of common coding theory. For example, common coding theory suggests that the shared representation is coded by action's perceptual consequences, which includes kinematics, targets and physical outcomes of an action. Neuroimaging studies support this coding principle on MNS. By using an elegant repetition suppression paradigm, Hamilton and Grafton (2006, 2007, 2008) demonstrated that MNS specifically codes the kinematics, targets and physical outcomes of an action. For example, they found that the anterior intraparietal sulcus, part of the parietal node of the MNS, codes the targets of an action (e.g. taking a cookie or a disk) (Hamilton and Grafton, 2006); inferior frontal gyrus codes the kinematics of an action (e.g. a precision grip or a power grip) (Hamilton and Grafton, 2007) and both frontal and parietal nodes code the physical outcome of an action (e.g. open or close a box) (Hamilton and Grafton, 2008).

In summary, the studies of mirror neurons in both monkeys and humans suggest that action observation and execution are commonly coded in the neural level, and the coder is the perceptual consequences of that action. However, several important questions regarding development arise: are action observation and execution commonly coded from the birth? Where do mirror neurons come from? Are we born to have mirror neurons? Associative sequence learning theory (ASL) suggests not.

Associative Sequence Learning theory

ASL theory explains the origin of the common coding framework, how mirror neurons are able to match observed and performed actions, and how individuals are able to mimic others' actions. It was proposed by Cecilia Heyes

(2001, 2010) and emphasizes the importance of learning and experience in generating the potential for mimicry.

As I mentioned in section 1.1.6, nativists believe that mimicry and its underlying mechanism (i.e. mirror neurons) have important survival value and social function; therefore they are innate and stored in the species' genome. As one of the famous empiricist theories, the ASL theory suggests that mimicry and mirroring mechanism are not evolutionarily selected for a specific function; instead it is a byproduct of the operation of domain-general associative learning, the same mechanisms that produce Pavlovian conditioning (Heyes, 2001; Bird and Heyes, 2005). Specifically, it claims that associations between sensory and motor representations are acquired through correlated sensorimotor experience—concurrent observation and execution of the same actions (with contiguity and contingency, see Cook et al., 2010). For example, when an individual is clenching his fist, the activation of the motor representation (the motor plan to clench fist) is always paired with the corresponding perceptual representation (the sight of a closed fist). The ASL theory proposes that, over time, a bidirectional associative link is formed such that activation of one representation excites the other (Heyes, 2010).

The above example illustrates the sensorimotor experience in a self-observation fashion. However, this does not apply to the development of sensorimotor associations for so-called 'perceptually opaque' actions such as facial expressions and whole body actions (e.g. dancing), because these opaque actions cannot be fully observed by self. The ASL theory proposes three other sources of sensorimotor experience to account for the emergence of associations for opaque actions: experience of using optical mirror

reflections, the experience of being imitated by others, and synchronous activities involved in sports and dance training (Ray and Heyes, 2010). For example, when an individual is taking a dancing class in front of a large gym mirror, she can see her own body movements either from the mirror or from synchronous movements performed by her classmates. Consequently, the motor representation of a dance is paired with the corresponding sensory representation (the sight of the dance from the mirror or others).

The most important characteristic of the ASL model is its emphasis on the uniqueness of sensorimotor experience to the formation of mirror neurons and mimicry (Heyes, 2010). It suggests that the only way that can create and influence the association between a sensory and a motor representation of action is through the correlated sensorimotor experience. Once the association is established, activation of the sensory component inevitably results in activation of the motor component (Heyes and Bird, 2007). This automaticity of sensorimotor mapping cannot be changed by any other cognitive processes except sensorimotor experiences. This means that if mimicry is modulated by a factor other than sensorimotor experiences, the modulation must not be mediated by directly interfering with the propagation of activation from the sensory to the motor component of a vertical association; modulation of mimicry is only allowed to be mediated by either influencing the sensory component or the motor component of a vertical association (Catmur et al., 2009).

The ASL theory gains strong empirical support from data showing that the magnitude of mimicry and the neural activation of mimicry can be changed and even reversed by sensorimotor training (see 1.2.6). Moreover, the theory

is compatible with evidence suggesting that the neural activations of mimicry are greater when an observer has more past sensorimotor experiences of that action (Calvo-Merino et al. 2005; 2006). For example, Haslinger et al. (2005) presented expert pianists and nonpianist controls with sequences of matched finger movements either similar or dissimilar to piano playing. They found that observation of the piano-related stimuli elicited a stronger fMRI response in classical mirror areas (IFG and IPL) in the pianists, but not in the non-pianist controls. Similarly, a stronger fMRI response was observed in classic MNS areas when ballet experts observed ballet sequences, than when they viewed matched non-ballet (i.e. capoeira) stimuli. The fact that mirror system activation is sensitive to sensorimotor expertise provides a strong indication that mimicry is acquired through learning.

1.2.7 Neural Mechanism of Mimicry

Neural Mechanism of Mimicry per se

Substantial evidence suggests that MNS is the neural mechanism of mimicry (Rizzolatti, 2005). Several studies on neuropsychological patients suggest that an intact MNS is essential to functional imitation. For example, lesions to the left inferior parietal lobe often result in apraxia—a deficit in miming gestures and in imitation (Wheaton and Hallett 2007). Lesions to the inferior frontal cortex also result in imitation deficits (Goldenberg et al. 2007). Interestingly, it seems that lesions to different parts of MNS can result in different imitation deficiency. For example, imitation of finger movements was impaired following lesions to the left IFG, while left inferior parietal lesions resulted in impaired imitation of hand postures (Goldenberg and Karnath,

2006). These findings suggest that MNS is critical to imitation.

As mimicry is a tendency to copy the observed actions, neuroimaging research investigates the neural mechanism of mimicry by using an action observation paradigm where participants passively observe photos or videos of human movements. In an early fMRI study by Iacoboni et al. (1999), participants were required to complete three tasks: observe finger movements only (mimicry condition), or copy the finger movements they saw (intentionally imitation condition), or perform pre-specified finger movements in response to a simple spatial cue (action execution condition). The results showed that the brain activity was stronger during mimicry and imitation conditions than during the action execution conditions in three MNS relevant areas: the left IFG, the right anterior parietal cortex and the right STS region (STS is the sensory input of MNS; see Rizzolatti and Craighero, 2004). Further experiments by Koski et al. (2002) and Grezes et al. (2003) obtained similar results.

Nishitani and Hari (2000, 2002) conducted two MEG studies in which they investigated mimicry of hand and lip movements. The first study confirmed the importance of the left IFG in the mimicry of grasping actions. In the second study, the authors asked volunteers to observe still pictures of verbal and nonverbal (grimaces) lip forms (facial mimicry condition), to intentionally imitate them immediately after having seen them (intentional imitation condition), or to make lip forms in a self-paced manner (orofacial gesture execution condition). They found that, during facial mimicry conditions, cortical activation progressed from the occipital cortex to the superior temporal region, the inferior parietal lobule, left IFG, and finally to the primary motor cortex. The activation sequence during intentional imitation was the same as during

mimicry. Instead, when the volunteers freely executed the lip forms (orofacial gesture execution condition), only the premotor and motor cortex were activated.

Perhaps the most convincing evidence for the MNS as the neural mechanism of the mimicry effect comes from Catmur et al. (2008, 2009). In one fMRI study, they required participants to do a sensorimotor training (see. 1.2.5. sensorimotor experience) and then used the hand opening/closing task (see 1.2.1) to measure mimicry effect. Previous studies showed that certain sensorimotor training can eliminate or even reverse the mimicry effect (Heyes et al., 2005). They found when the mimicry effect was reversed by the training tasks, the activity of MNS was also correlatively reversed by the training. In another study, they examined whether virtual lesion to the MNS influences the mimicry effect. They used a new rTMS protocol, continuous theta-burst stimulation, to disrupt IFG functioning during a SRC task. The results showed that theta-burst rTMS of the left IFG abolished the mimicry effect, suggesting that the left IFG plays a causal role in mimicry. Therefore, these findings provide direct evidence that MNS is the neural mechanism of mimicry effect.

Neural Mechanism of inhibition of Mimicry

To some degree, mimicry is a prepotent response tendency—observing an action automatically and unintentionally triggers the tendency to execute that action. However, since it is obvious that mimicry is not adaptive in many everyday situations, the question that arises is how such tendency to mimicry is prevented from leading to overt mimicry behaviour.

Early clinical observation suggests that the inhibition of inappropriate

response tendencies is a function of the frontal lobes. Patients with frontal lesions sometimes have difficulties in tasks involving inhibition of prepotent responses, such as Stroop task and the go/no-go or stop-signal paradigm (Luria, 1980; Vendrell, 1995). With regard to the inhibition of mimicry, Luria (1980) devised a task in which patients were required to execute one action (making a fist) in response to the observation of a different action (showing the finger) and vice versa. He reported that patients with prefrontal lesions show the so-called echopractic responses: they tended to mimic the observed action while ignoring the verbal command. Such inability to inhibit mimicry tendency following prefrontal lesions have also been reported in patients with a syndrome called imitation behaviour (Lhermitte et al., 1986; De Renzi et al., 1996). Patients showed overt imitative response tendencies, even when they were told to stop imitating. However, which prefrontal lesions cause imitation behaviour is still controversial.

Compared to the investigations of mimicry, not many fMRI studies have been conductied on the inhibition of mimicry so far. For example, Brass et al., (2001a, 2005) used a finger tapping task in which subjects were instructed to execute predefined finger movements (tapping or lifting of the index finger) in response to an observed congruent or incongruent finger movement (tapping or lifting). A comparison of brain activation in incongruent and congruent trials revealed strong activation in two areas: medial prefrontal cortex (mPFC) and temporal-parietal junction (TPJ). These two regions are different from the systems responsible for the Stroop task (e.g. dorsolateral PFC, ACC), which suggests that inhibition of mimicry is not related to classic cognitive control (Brass et al., 2005).

mPFC and TPJ are two brain regions strongly engaging in theory of mind (ToM) tasks (Frith and Frith, 1999). Considering that ToM tasks require the ability to focus on one's own mental states while suppressing others' (Gallagher et al., 2000), Brass et al. (2009) proposed that the inhibition of mimicry involves processes for self-other distinction. They did several behavioural studies to test this idea. In the first study, Spengler et al., (2010a) implemented the 'finger tapping task' and the classic ToM tasks in both healthy participants and neuropsychological patients with prefrontal lesions or TPJ lesions, to examine whether there is a functional association between the inhibition of imitation and self-other distinction. The results showed a highly significant correlation between imitative control and the abilities to mental attribution in both health participants and patient with lesions. In order to rule out the possibility that the correlation is mediated by classic cognitive control, all healthy participants and patients were required to complete the Stroop task. Even after controlling for executive functions, the results remained significant, indicating the functional specificity of this relationship. In a second study, Spengler et al. (2010b) implemented the same experiment design on individuals with autism, who were traditionally believed to have impairments of self-other distinction. Similar to those patients with prefrontal or TPJ lesions, the results suggest that the ability of mental attribution in individuals with autism was positive correlated with their inhibition of mimicry: the worse individuals with autism behaved in the ToM tasks, the less they were able to inhibit their mimicry tendency. In a third study, Spengler et al. (2010c) directly manipulated the processes for self-other distinction when healthy participants were performing the finger-tapping task. In half of the blocks, participants were

asked to do the task in a self-focus condition where two mirrors were placed on each side of the monitor, so that participants could see their face and upper part of the body reflected in the mirror. In the other half blocks, the mirrors were turned around with the noon-reflective side facing the subjects (no self-focus control condition). Results showed that comparing with no self-focus condition, participants showed reduced mimicry during self-focus conditions, which reflects an enhanced inhibition of mimicry. The findings in these three studies suggest that inhibition of mimicry is associated with the processes for self-other distinction.

1.2.8 Summary of Mimicry Research in Cognitive Neuroscience

In the second half of the introduction chapter, we reviewed the research of mimicry effect in cognitive neuroscience. Past research adopted SRC paradigms to investigate the relationship between action and perception and found that mimicry effect is based on a direct link from perception to action. Mimicry effect has impacts on cognitive functions such as emotional recognition and person perception, and can also be modulated by other cognitive processes such as arousal, attention, animacy and sensorimotor experience. Several theoretical frameworks have been proposed on the mechanism of mimicry. The most popular one suggests that mimicry effect is based on a common-coding principle between action and perception and mirror neurons are the neural substrate of this principle. The ASL theory further suggests that this common-coding principle is formed by associative sequence learning from sensorimotor experience. Neuroimaging studies

revealed that MNS is the neural substrate of mimicry effect whereas mPFC and TPJ are the neural substrate of inhibition of mimicry (see Figure 1-4).
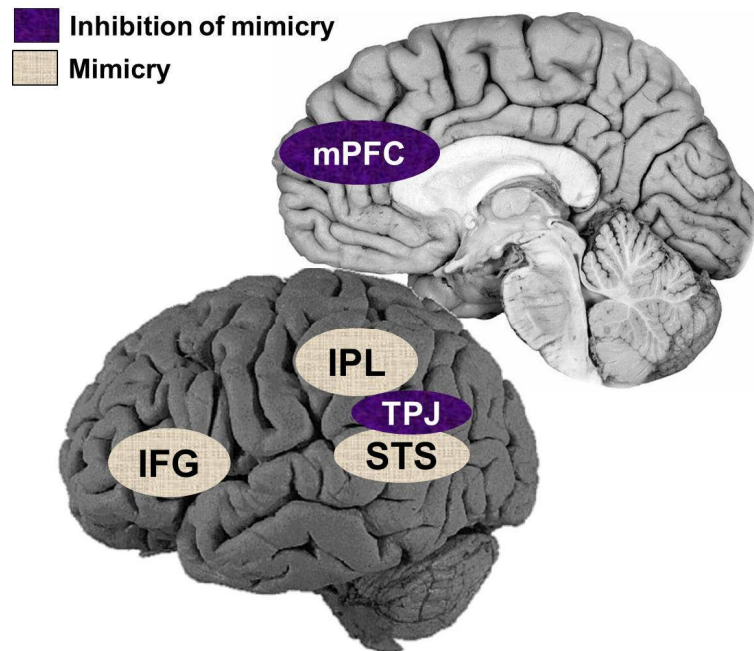
Figure 1-4. Neural Substrate of Mimicry and Inhibition of Mimicry. Substantial neuroimaging evidence suggests that human MNS is the neural substrate of mimicry. Mimicry tasks engage the activations of inferior frontal gyrus (IFG), inferior parietal lobe (IPL) and superior temporal sulcus (STS). In contrast, research suggests that the inhibition of mimicry involves a different neural system, which includes medial prefrontal cortex (mPFC) and temporal-parietal junction (TPJ).

1.3 Summary of Experimental Chapters

As reviewed, social psychology and cognitive neuroscience investigate mimicry in different perspectives. They both have pros and cons in research scopes and methodologies. Specifically, social psychology primarily examines the visible mimicry behaviour and its changes according to social contexts, but ignores the neural mechanism underlying this behavioral mimicry and its modulations. In contrast, cognitive neuroscience mainly focuses on the underlying mechanism of mimicry but ignore the social significance of mimicry and its modulation by social factors. In methodologies, social psychology uses naturalistic paradigms to study real 'mimicry', but poorly controls individual differences and different variables in the contexts. Also, naturalistic paradigms are not sensitive to rapid and temporary modulators. On the contrary, cognitive neuroscience uses simple and well-controlled SRC paradigms to measure the invisible mimicry tendency. Participants have to repetitively perform simple movement in a context-constrained lab environment. This setting forgets the fact that mimicry per se is a social behaviour.

The purpose of the PhD project is to investigate the control of mimicry by social signals. It aims to examine how people mimic according to different social signals and what is the neural mechanism of the control of mimicry. In methodologies, this project integrates those pros in social psychology and cognitive neuroscience, and introduces the well-controlled SRC paradigms in a social context.

Specifically, the studies in this thesis aim to address the following five questions:

1) *Can mimicry be rapidly modulated by critical social signals such as eye gaze?*

Chapter 2 shows that direct gaze rapidly and specifically enhances mimicry.

2) *Is the control of mimicry by eye gaze due to an attentional effect?*

Chapter 3 shows that the enhancement of mimicry by direct gaze is not due to any non-social effects. Rather, it is the social cue of eye contact itself that drives mimicry.

3) *What is the neural mechanism of this control of mimicry by eye gaze?*

Chapter 4 shows that medial prefrontal cortex is the originator of this eye contact effect on mimicry. It works with MNS to control mimicry according social contexts.

4) *Is mimicry in social contexts stimulus-driven or strategic-based?*

Chapter 5 shows that mimicry in social contexts works in a Machiavellian fashion. Social status and niceness strategically modulate mimicry.

5) *How does social priming modulate mimicry?*

Chapter 6 shows that self-relatedness plays an important role in the social priming effect of mimicry.

Chapter 2. Eye contact enhances mimicry of intransitive hand movements

2.1 Abstract

When two people meet in a bar, a subtle interplay of social behaviours, including eye contact and unconscious mimicry of actions plays an important role in how much the individuals like each other by the end of the evening. However, it is not known how these different social signals interact. In this Chapter, we adopt a rapid SRC paradigm, to test if eye contact can modulate mimicry on a second by second timescale. Two experiments consistently show that direct gaze rapidly and specifically enhances mimicry of hand actions and this effect is not due to spatial attention. These findings reflect the flexibility and subtlety of mimicry in social contexts and have implications for understanding the role of eye contact as a controlling signal in human nonverbal social behaviour.

2.2 Introduction

Chapter 1 reviewed that human mimicry is an unconscious form of imitation which facilitates social interaction. There is a close relationship between mimicry and affiliation. Interactions with more mimicry lead to more liking and affiliation (Chartrand and Bargh, 1999), while interactions with an affiliation goal are characterized by more mimicry (Lakin and Chartrand, 2003). Motivation and emotion can also foster or inhibit mimicry (Chartrand and van Baaren, 2009). However, all these effects (in social psychology studies) take

place over minutes or hours; it is not known if faster, more direct modulation of mimicry is possible.

Like mimicry, eye contact is an important signal in non-verbal communication and social interaction (Senju and Johnson, 2009). In two-person settings, people spend 31% of the time engaging in mutual gaze, and each mutual gaze lasts around a second (Argyle and Ingham, 1972). Increased eye contact is associated with increased liking and affiliation (Mason, et al., 2005), and with better performance on tasks such as face detection (Conty et al., 2006), gender discrimination (Macrae et al., 2002) and identity encoding/decoding (Hood et al., 2003).

Although mimicry and eye contact both play a pivotal role in social interaction and are both linked to liking and affiliation, the relationship between the two remains unclear. Some theories (Csibra and Gergely, 2009) suggest that eye contact is a critical social signal for imitation, with a controlling role, but other approaches focus on the relationship between mimicry and affiliation without emphasizing other social signals (van Baaren et al., 2009). Past research on eye contact and action has found that observed gaze can influence the kinematics of motor performance (Castiello, 2003) and neural response to observed action (Kilner et al., 2006). However, these studies did not directly examine mimicry.

In the present chapter, we aimed to link studies of eye contact and mimicry, and to test if eye contact can rapidly and directly modulate action mimicry. We adopted a SRC paradigm (the 'hand opening/closing' task, see 1.2.1) used by Heyes and colleagues (Heyes et al., 2005), in which participants respond to a hand-opening or hand-closing stimulus by either

opening or closing their own hand. Previous research found faster responses to congruent than incongruent actions and took this congruency effect as a measure of mimicry. In the present experiment, an eye contact priming movie was introduced before each trial of the 'hand opening/closing' task, to examine whether direct eye gaze can influence the congruency effect.

2.3 Experiment 1: Does eye contact modulate mimicry?

2.3.1 Materials and Methods

Participant

Twenty right-handed students from University of Nottingham participated in this study (19 females, 1 male; mean age=22.6 years; *SD*=3.15 years).

Stimuli and Apparatus

Before each trial, a fixation cross was presented for 300 msec. Then a 2.5 seconds video of human head movement was used as the gaze priming movie for each trial (Figure 2-1). At the onset of each video clip, participants saw a female actor facing away from the camera, with her eyes closed and her left hand still in front of her face. Then the actor opened her eyes, naturally moved her head either towards the camera which resulted in a direct gaze, or towards her left/right side which resulted in an averted gaze; her hand remained entirely still. Subsequently, her hand opened or closed. Delay between the end of head movement and the start of hand action was 200 or 800ms and the hand movement stimulus had a duration of 200ms. Video editing software was used to precisely match the timing and actor motion parameters between stimuli. All stimuli were presented on a 20" size computer

monitor and were 18.8 cm by 12.5 cm on the screen.
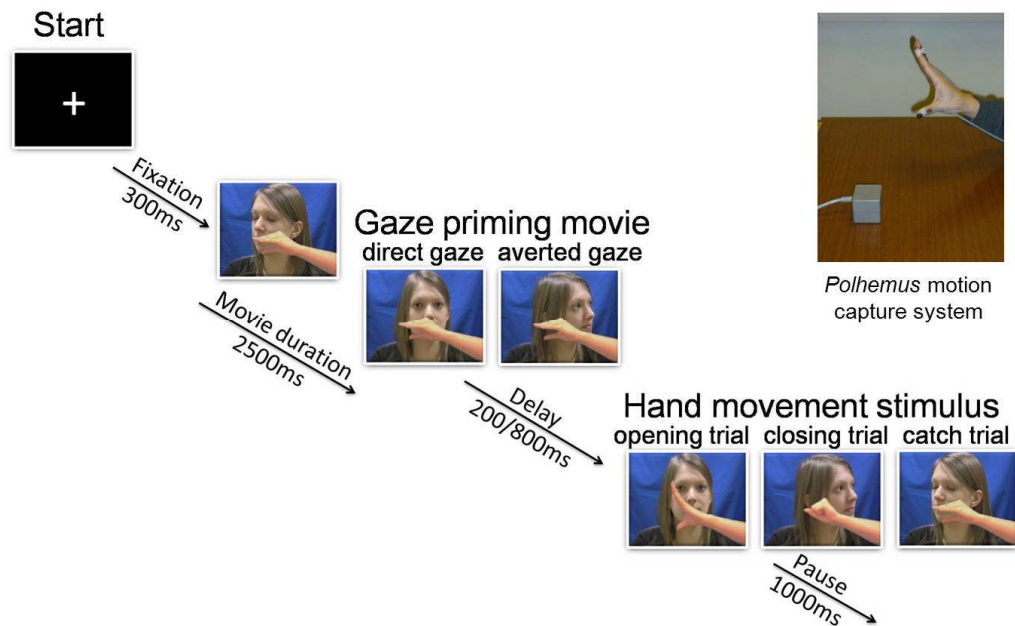
Figure 2-1. Examples of the stimuli and sequence of events in Experiment 1. At the beginning of each trial, participants observed a gaze priming movie where a direct or averted gaze was provided by the actress. After an unpredictable delay (200 or 800ms), they had to perform a pre-specified hand movement in response to a hand action stimulus by the actress, as fast as they can. Pholemus motion capture system was used to record the reaction time of hand responses.

Design and procedure

The experiment used a rapid SRC paradigm—the 'hand opening/closing task' (Heyes et al., 2005). For each block, participants were required to make the same pre-specified response (to open or close their right hand) in every trial, as quickly as possible after the actor's hand in video clips began to move. On some trials, the actor's stimulus hand opened and on others it closed. Therefore, within a block, the hand movement stimulus was either the same as the pre-specified response (congruent trials, e.g. open stimulus and open

response) or the opposite of the pre-specified response (incongruent trials, e.g. close stimulus and open response). Participants were instructed to respond as quickly as possible in all trials. Response movement direction was orthogonal to stimulus movement direction to avoid spatial compatibility confounds (Press et al., 2008).

There were 4 blocks and 240 trials in total; two blocks required hand-close response and two blocks required hand-open response. Block order alternated and was randomized across participants. Each block presented, in random order, 48 stimulus trials (where actor's hand opened/closed) and 12 catch trials (where actor's hand kept still). Participants were instructed to refrain from moving their hand in catch trials.

There were 3 stimulus trials of each type, defined by 2×2×2 factorial design: direction of eye gaze (direct or averted), stimulus hand action (opening or closing) and delay (200 or 800ms). Variable delays were used to prevent anticipatory responses but were not analyzed further.

Reaction time (RT) was measured by an electromagnetic device (Polhemus LIBERY system, Colchester, USA) (Figure 2-1). Two sensors were taped on the thumb and middle fingernail of participants' right hand and the sensor's spatial position was recorded at 240Hz. Finger and thumb location data were recorded in Matlab, which also controlled presentation of the video and still image stimuli via the Cogent toolbox. Hand aperture was calculated as the distance between thumb and figure markers. Aperture velocity was calculated and then smoothed with a 40 msec square window. Peak velocity was defined as the first peak in the velocity profile which reached at least 60% of the largest peak. This allowed us to exclude rare "wobbles" in the data and

pick the initial fast hand opening or closing movement. RTs were calculated as the time from the presentation of the 2nd frame of the hand movement video to the time when the participant's hand aperture reached its first peak open/close velocity.

2.3.2 Results and Discussion

To remove trials in which participants did not attend to the hand stimuli, incorrect responses (0.05%) were excluded from the analysis, as were all RTs smaller than 100ms or greater 800ms (0.10%). To minimize the effect of outliers, we also excluded RTs that were greater than two standard deviations from the conditional means of each participant (0.10%).

RT data were analyzed with a two-way repeated measures analysis of variance (ANOVA) on the factors of Congruency (Congruent vs. Incongruent hand movement) and Direction (Directed vs. Averted gaze). The analysis revealed a significant main effect of Congruency ($F(1,19)=41.0$, $p<0.001$) and Direction ($F_{(1,19)}=24.2$, $p<0.001$); Importantly, there was an interaction between Congruency and Direction ($F_{(1,19)}=10.3$, $p<0.005$) (Figure 2-2). Furthermore, a post hoc t-test showed that congruent responses were faster when preceded by direct gaze than by averted gaze ($t_{(20)} = 6.18$, $p<0.001$), but incongruent responses were statistically unaltered whenever preceded by direct or averted gaze.
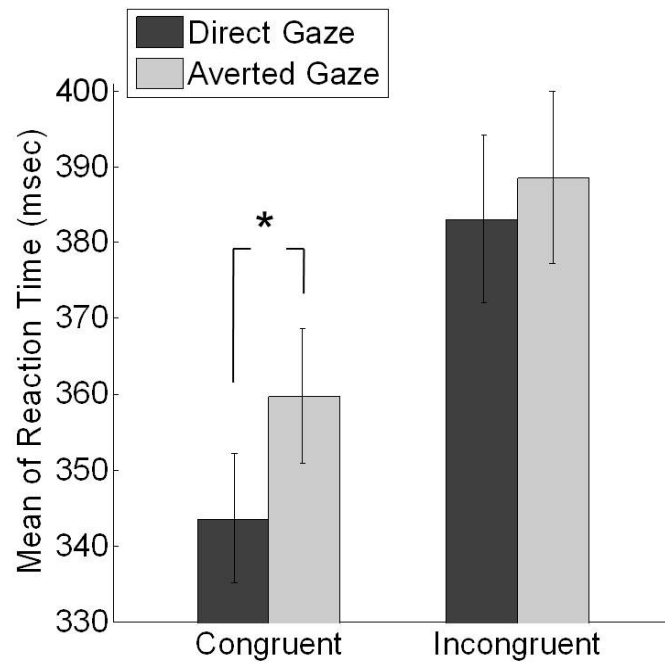
Figure 2-2. Mean RT on congruent and incongruent trials, for direct and averted gaze conditions in Experiment 1. "*" represents the statistically significant difference between two bars and vertical bars indicate S.E.

The results from this experiment indicated a facilitatory effect of eye contact on mimicry and more importantly revealed a significant interaction between eye contact and mimicry. That is, direct gaze enhanced the reaction times for congruent trials compared to incongruent trials, while averted gaze did not. This rapid modulation of mimicry by gaze is novel and provides a potent mechanism for social interaction. However, this first experiment did not control for the possibility that, in the averted gaze conditions, the participant's visual attention was distracted away from the centre of the display and this change in visual attention could contribute to the observed effects. We addressed this question in Experiment 2, in which an eye-catching white box suddenly flashed on the screen before the hand movement to draw attention in a new control condition.

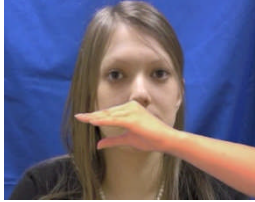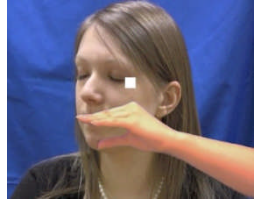## 2.4 Experiment 2: Is this modulation due to spatial attention?

2.4.1 Materials and Methods

Participants

Twenty-three right-handed students, who did not participant in Experiment 1, participated in this study (12 females, 11 males; mean age=23.7 years; *SD*=3.01years).

Stimuli

Half the trials in Experiment 2 used exactly the same gaze stimuli as Experiment 1. The other half used three new flash-box priming conditions (Figure 2-3). In these movies, the female actor kept her eyes closed and head averted throughout. 2380ms after the movie started, a small white box (0.8cm x 0.8cm) appeared in a central location or to the left or right of centre, level with the actor's eyes. The rapid appearance of a visual stimulus is known to trigger an automatical attentional response (Posner, 1980). The box disappeared after 120ms, and the whole movie lasted 2500ms, the same time amount as the head movement in gaze priming condition. After the flashbox disappeared, there was a delay of 200 or 800 msec before the actor began to perform a hand opening or hand closing movement, as before. Stimulus presentation and data recording were identical to Experiment 1.

	Direct/Central	Averted / Peripheral
Gaze Conditions		
Flashbox Conditions		

Figure 2-3. All types of priming stimuli in Experiment 2. In addition to experiment 1 where three gaze priming conditions were provided (direct gaze and right/left averted gaze), Experiment 2 added another three flash-box priming conditions (central box and right/left peripheral box).

Design and procedure

The procedure was similar to the procedure in Experiment 1 except for the number of trials. In the testing part, there were 8 blocks and 320 trials in total. Participants had to give hand closing response in four blocks and hand opening response in the other four (order was randomized). Each block presented, in random order, 32 stimulus trials (where actor's hand opened/closed) and 8 catch trials (where actor's hand kept still). There were 2 stimulus trials of each type, defined by 2×2×2×2 factorial design: priming (gaze or flash-box), direction (direct or averted), stimulus hand action (opening or closing) and delay (200 or 800ms).

2.4.2 Results and Discussion

The same procedure as Experiment 1 was implemented on raw RT data, to remove incorrect responses (0.07%) and RT outliers (0.20%). Possibly due to an increased ratio of male participants from Experiment 1 (1 male and 19 femals) to Experiment 2 (11 males and 12 females), the overall RT in Experiment 2 (290-320ms) was faster than in Experiment 1 (340-390ms) (Figure 2-4).

RT data were analyzed with a three-way ANOVA on the factors of Priming (Gaze vs. Flash-box), Congruency (Congruent vs. Incongruent) and Direction (Direct/Central vs. Averted/Peripheral). The analysis revealed a significant main effect of Priming ($F_{(1,22)}$=4.34, p<0.043), Congruency ($F_{(1,22)}$=29.5, p<0.001) and Direction ($F_{(1,22)}$=21.2, p<0.001) and three significant interactions, Congruency × Priming ($F_{(1,22)}$=5.20, p<0.027), Direction × Priming ($F_{(1,22)}$=7.58, p<0.008) and Congruency × Direction × Priming ($F_{(1,22)}$=4.16, p<0.047).

To explore these interactions fully, gaze priming data and flash-box priming data were separately analyzed with a two-way ANOVA on the factors of Congruency (Congruent vs. Incongruent) and Direction (Directed/Central vs. Averted/Peripheral). The analysis of gaze priming data revealed a significant main effect of Congruency ($F_{(1,22)}$=18.4, p<0.001) and Gaze direction ($F_{(1,22)}$=21.8, p<0.001) and the critical interaction between Congruency and Gaze direction ($F_{(1,22)}$=10.8, p<0.003) (Figure 2-4). As before, a post-hoc t-test suggested that congruent movements were faster when primed by direct gaze than by averted gaze ($t_{(23)}$ = 5.37, p<0.001).

In contrast, the analysis of flash-box priming data only revealed a significant main effect of Congruency ($F_{(1,22)}=8.09$, $p<0.009$); No other factors reached the significant level, including the non-significant interaction between Congruency and Flash-box direction ($F_{(1,22)}=0.174$, $p=0.681$) (Figure 2-4).

The results from Experiment 2 replicated Experiment 1 with a new group of participants and show that drawing attention to the side of the display with a non-social cue does not impact on mimicry. Although criticism could be still built on the trivial spatio-temporal differences between flash-box conditions and eye gaze conditions, we believe that the results in Experiment 2 are sufficient to suggest that the enhancement of mimicry that we observe is specific to eye contact and is not driven by spatial attention
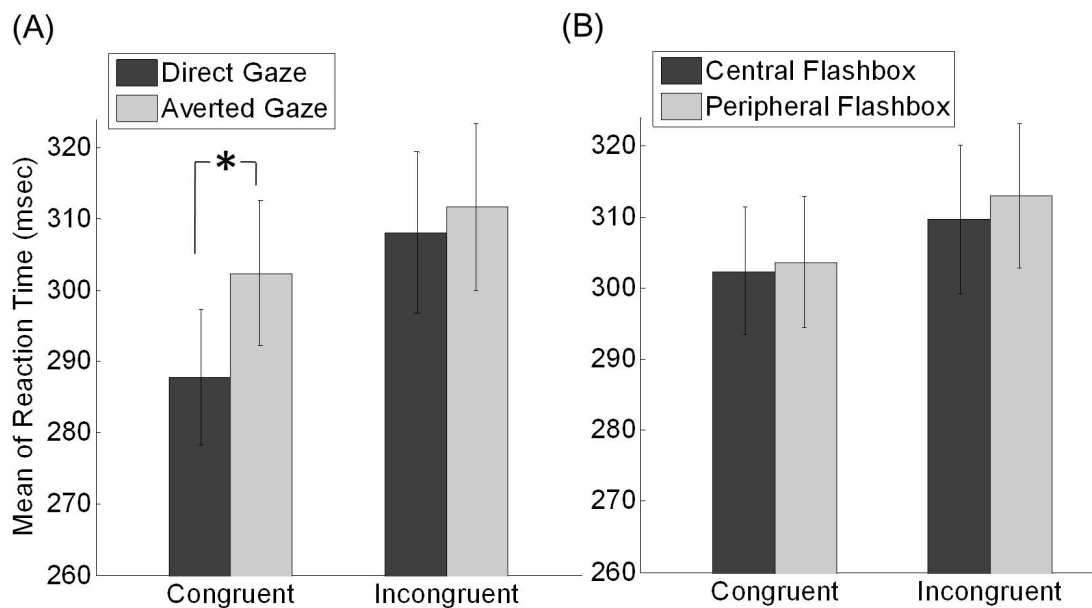
Figure 2-4. Mean RT on congruent and incongruent trials for **(A)** Gaze conditions and **(B)** Flash-box conditions. "*" represents the statistically significant difference between two bars and vertical bars indicate S.E.

2.5 General Discussion

These two experiments provide strong evidence that eye contact rapidly and specifically enhances mimicry of hand actions. In both experiments, responses to congruent actions were faster when preceded by direct gaze.

Underlying Mechanism of the eye contact effect on mimicry

To understand the origins of the eye contact effect, we first exclude possible non-social mechanisms. The effect of eye contact on mimicry was not a general arousal effect, because incongruent response times were unaltered (Figure 2-4A). We also controlled for spatial attention. Previous studies reported that observing another person's averted gaze automatically shifts spatial attention (Friesen et al., 2005). If the averted gaze draws attention away from the centre of the screen, this might impact on mimicry. However, our flash-box control condition in Experiment 2 shows that distracting stimuli at the side of the display do not impact on mimicry (Figure 2-4B). Also, changes in spatial attention would not predict an enhancement that is specific to congruent actions, as we found in gaze condition. Similarly, our results reflect more than just a general increase in arousal due to eye contact, because we found a specific enhancement for congruent actions compared to incongruent ones. Thus, we conclude that our results reveal a novel and powerful social mechanism whereby eye contact rapidly enhances action mimicry.

Our data shows that direct-gaze congruent-action condition resulted in faster reaction times than any other conditions. However, the direct-gaze incongruent-action condition was not slower than the averted-gaze

incongruent-action condition (Figure 2-4A). Why is the modulation of mimicry by eye contact specific to the enhancement of congruent trials, but not to the inhibition of incongruent trials? We suggest that this could reflect a double eye contact effect. First, it is possible that eye contact enhances all reaction times, as an alerting stimulus. Second, eye contact has a specific impact on mimicry, facilitating congruent responses and slowing down incongruent ones. Considering these two effects together predicts a rapid reaction in the direct-gaze congruent-action condition, as found. In the direct-gaze incongruent-action condition, this alerting effect of eye contact would counteract the mimicry effect of eye contact, leading to no change in reaction time from the averted-gaze incongruent action condition. Future research is needed to support this explanation.

Implications for social cognition

Our finding has important implications for emerging ideas about nonverbal behavior in human social interaction. Our data are congruent with models which emphasis flexible control of imitation (Brass et al., 2009) and an influence of eye gaze on action understanding (Castiello, 2003; Kilner et al, 2006). We go beyond these studies in showing that a specific ostensive social cue – eye contact – enhances mimicry actions rather than incongruent actions.

Our results are also congruent with developmental studies that point to eye contact as a critical ostensive signal which modulates social learning. Infants are sensitive to eye contact from birth (Farroni et al., 2002) and learn more from situations with eye contact (Csibra and Gergely, 2009). As mimicry is a form of imitation and contributes to learning new skills, it is plausible that some of the enhancement of social learning by eye contact in infants and

possibly even in adults is mediated by mimicry. Our results provide clear support for the claim that eye contact is an important ostensive signal (Csibra and Gergely, 2009), and suggest that eye contact modulates behavior, not just in infancy, but throughout the lifespan.

Implications for autism research

Our results may have implications for our understanding of mimicry and imitation in autism. Clinical observations often report atypical patterns of mutual gaze behaviour in Autism Spectrum Disorder (ASD) and use this as part of the autism diagnosis. Some studies report a relative lack of an increased neurophysiological response to eye contact both in ASD adults and potential infants (Senju et al. 2005; Elsabbagh et al. 2009). Children and adults with autism also show reduced imitation (William et al., 2004), especially in naturalistic situations. This poor imitation has been attributed to failure of the mirror neuron system (William et al., 2001, Oberman et al., 2005), but could also be attributed to poor top-down control of mimicry (Hamilton, 2008). One interesting study addresses the interaction of gaze and mimicry, showing that hand actions in typical children can be primed by the actions of a live human model but not a robot. In contrast, hand actions in autistic children were only primed by the actions of the robot (Pierno et al. 2008). This suggests that live interaction, including possibly eye gaze, is important for mimicry in typical but not autistic children. Extending this, an important implication of our own data is that failure to make eye contact or to understand eye contact in autism might be a causal factor in reduced mimicry behaviors. Understanding the relationship between mimicry and eye contact in autism is an important area for future research.

Methodological Implications

Finally, it is also important to consider how our rapid SRC task relates to other more naturalistic mimicry paradigms used to study the "chamaeleon effect" (Chartrand and van Baaren, 2009). Our rapid paradigm puts participants in a very different context (van Baaren et al. 2009). However, in both naturalistic and rapid mimicry paradigms, participants are unaware that the experimenter is recording mimicry behaviors or that mimicry is the subject of the investigation. Studies of mimicry in naturalistic situations look at mimicry effects which occur over seconds (Oullier et al., 2008) and modulation of mimicry over minutes (Lakin and Chartrand, 2003), but this makes it hard to determine causal factors. Our approach allows us to measure response times with millisecond precision and obtain an estimate of the speed of the eye contact effect. The speed of the eye contact effect we report, with just 500ms between the eye contact event and the mimicry response, suggests it is not mediated by general changes in affiliation. Rather, we suggest that eye contact directly impacts on the mimicry process, and this could be a causal factor in the "chameleon effect" (Chartrand and Bargh, 1999, also see 1.1.3).

2.6 Conclusion

In conclusion, Chapter 2 has demonstrated that mimicry is a flexible nonverbal behaviour which can be subtly modulated by social signals. Direct gaze rapidly and specifically enhances unconscious mimicry. Our findings suggest that eye contact is a powerful controlling signal which induces more than just arousal and attentional effects on mimicry. Better understanding how gaze signal subtly enhances mimicry will help researchers learn more about human nonverbal behaviour in social contexts.

Chapter 3. More than just attention: Communicative gaze sequences guide one's tendency to mimic

3.1 Abstract

In Chapter 2, we found a behavioral gaze-mimicry interaction where direct gaze rapidly and specifically enhances the mimicry of intransitive hand movement. We also demonstrated that this effect is not due to a simple spatial attention effect. However, eye gaze is a powerful signal which exerts both social and non-social effects on the observer. Hence, the current chapter aims to systematically investigate which aspects of eye gaze contribute to this enhancement of mimicry. In order to dissociate the social and non-social effects of eye gaze on mimicry, we used a two-gaze-sequence priming video where an actress provided two gaze shifts before performing a hand movement. We manipulated the direction and sequence of the two gazes to induce different arousal, attentional and social effects on the subsequent hand movements. Our results suggest that different arousal and attentional effects by gaze sequences cannot influence one's tendency to mimic, but only the social messages of eye gaze modulate mimicry. These findings provide strong evidence that the eye contact effect on mimicry is driven by the social effects of eye gaze and help us better understand the mechanism of the control of mimicry by social signals.

3.2 Introduction

Eye gaze provides a foundation of communication and social interaction (Senju and Johnson, 2009). It conveys critical information about conspecifics' attention, interests and intentions. Past studies suggest that the mere perception of eye gaze increases arousal (Conty et al., 2010), triggers a reflexive shift of spatial attention towards the gaze direction (Friesen et al., 2005), directs joint attention to the objects of other's interest (Emery, 2000) and conveys ostensive social messages such as communicative intention and interpersonal interest (Kampe et al., 2003). Gaze is also a powerful controlling signal on other social-cognitive processes. Direct gaze significantly facilitates face detection (Conty et al., 2006), identity encoding/decoding (Hood et al., 2003), gender discrimination (Macrae et al., 2002) and person/object evaluation (Kampe et al., 2000; Mason et al., 2005; van der Weiden et al., 2010).

Mimicry is another important feature of human interaction. People have a tendency to unconsciously mimic others' actions (Chartrand and Bargh, 1999). This spontaneous mimicry facilitates social interaction and serves as an unconscious social strategy in creating social bonds between people (Chartrand and van Baaren, 2009). Although mimicry is not normally consciously controlled, extensive research suggests that mimicry is flexible and context-dependent (see 1.1.5 and 1.2.5). It is not only sensitive to low-level cognitive processes like arousal (Fujimura et al., 2010) and attention (Chong et al., 2009), but can also be modulated by high-level social factors such as social motivation (Chartrand and van Baaren, 2009). For example,

people who have a desire to affiliate with others have stronger mimicry than those who have a desire to disaffiliate with others (Lakin et al., 2003). People exhibit more mimicry when they were primed with a prosocial attitude than primed with an antisocial attitude (Leighton et al., 2010). Mimicry is also increased when people interact with those they like, such as friends, attractive targets, in-group members and high social status ones (Chartrand and van Baaren, 2009).

In Chapter 2, we found behavioral evidence that mimicry can be rapidly modulated by gaze directions in a simple hand movement task. Participants observed a hand movement preceded by a direct or averted gaze and concurrently performed a congruent or incongruent hand movement. Our results showed that direct gaze significantly enhances the mimicry of the hand movement compared to averted gaze. This result supports previous findings suggesting that eye gaze is a powerful controlling signal and mimicry is sensitive to social signals. However, as direct gaze is a complex signal not only triggering non-social arousal and attentional effects but also conveying critical ostensive social messages such as communicative intention and interpersonal interest (Senju and Johnson, 2009), it remains unknown which specific effect of eye gaze contributes to the eye contact effect on mimicry. The current study aims to clarify this question.

Different from the paradigm in Chapter 2 where a single direct or averted gaze was provided right behind the hand stimuli, here we presented gaze shifts a distance away from the hand stimuli and used a novel two-gaze-sequence priming video to dissociate the social and non-social effects of eye gaze on mimicry (Figure 3-1B). Participants watched videos where an actress

would provide two gaze shifts and a hand movement. Specifically, she would look either at the side (an averted gaze), or the camera (a direct gaze), or her own hand (a hand gaze) during the first and second gaze shift and then perform a hand opening or closing movement. Therefore, according to the first and second gaze direction, the actress would provide nine types of gaze sequence videos before the hand movement (Figure 3-1A).

Because each type of the gaze sequence videos brings different social and non-social effects of eye gaze, this new paradigm provides a direct way to examine which social or nonsocial effect of gaze causes for the enhancement of mimicry. Specifically, we hypothesized that if the eye contact effect onmimicry is due to a general arousal effect of direct gaze, we should observe a stronger mimicry whenever the gaze sequence includes a direct gaze (either in the first or second gaze); if the effect results from spatial attention, we would expect to see increased mimicry whenever the second gaze was presented towards the space of hand side (e.g. a hand gaze or a rightward averted gaze); if direct gaze enhances mimicry by eliciting the joint attention towards the hand, we would see a larger mimicry in those gaze sequences ended by a hand gaze, probably the largest one when the first gaze is a direct gaze and the second is a hand gaze. Finally, if the enhancement on mimicry is not from any attentional or arousal effects to the hand, but only comes from the social messages of direct gaze such as ostensive communicative intention and personal interest, we hypothesized that participants should have an increased mimicry only when the second gaze is a direct gaze.

3.3 Materials and Methods
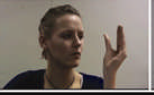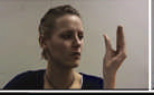
Participants

Twenty paid right-handed students participated in this study (15 females, 5 males; mean age = 21.4 years; S.D. 2.23 years).

Stimuli and Apparatus

In each trial, participants watched a video where an actress performed a sequence of two gazes and then a hand movement (Figure 3-1). At the onset of each video clip, the actress kept her eyes closed and held her left hand still on the right side of the screen. Her head was facing towards three possible directions: left sideways, straightforward, or rightward to her left hand. Then the actress opened her eyes and provided the first gaze along her face orientation for 500ms, which could be an averted gaze to the left side (AG-1), or a direct gaze to the camera (DG-1), or a hand-oriented gaze (HG-1). Her face was emotionally neutral during the first gaze. Subsequently, the actress naturally turned her head to other directions and provided the second gaze, which could be a new averted gaze towards right side (AG-2), or a new direct gaze to the camera (DG-2) or a new hand-oriented gaze (HG-2). The actress also provided a little smile along with the second direct gaze (DG-2), which was designed to strengthen the ostensive nature of direct gaze. After the two gaze shifts, the actress' hand began to move. She either opened her hand or closed her hand (stimulus trials), or remained hand static (catch trials). Delay between the end of second gaze and the start of hand action was 200 or 800ms and the hand movement stimulus had a duration of 1000ms. Video editing software was used to precisely match the timing and actress motion

parameters between stimuli.

(A) Experimental Design for the Two-Gaze-Sequence Priming Movie

(B) Timeline for the Two-Gaze-Sequence Priming Movie
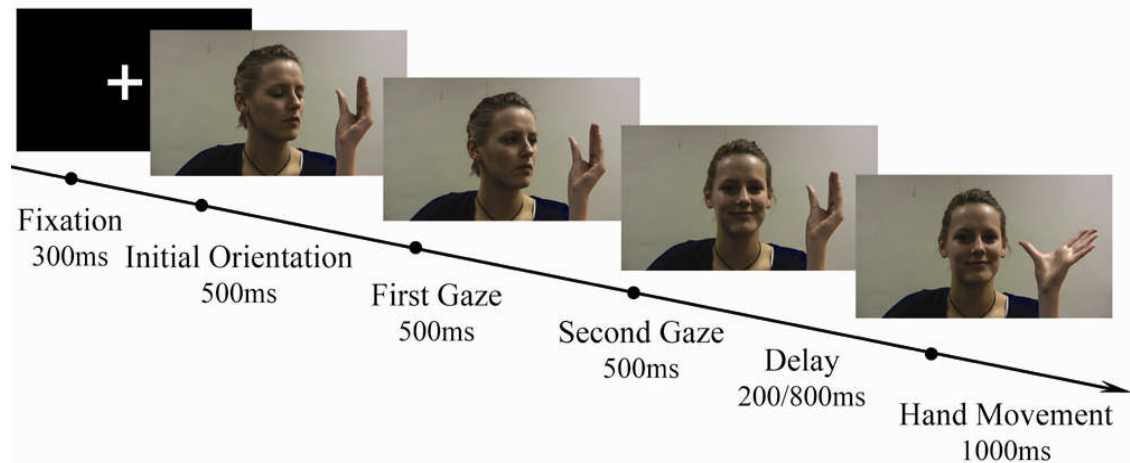
Figure 3-1. Experimental design (A) and Timeline (B) for the two-gaze-sequence priming movie. Participants were shown a series of 4 s videos clips where an actress did two gaze shifts and a hand movement. We adopted a 3×3 factorial design to present the two gaze shifts, where the actress either looked at the camera or sideways or her hand in the first and second gaze. After the two gazes, the actress performed a hand opening or hand closing movement.

Procedure

The experiment used an established SRC paradigm (the 'hand opening/closing task') to measure mimicry. For each block, participants were required to make the same pre-specified response in every trial. They had to

always open or close their right hand as quickly as possible after the actress' hand in the two-gaze-sequence videos began to move. On some trials, the actress' hand opened and on others it closed. Therefore, within a block, the hand movement in the movie was either the same as the pre-specified response (congruent trials, e.g. open stimulus and open response) or the opposite of the pre-specified response (incongruent trials, e.g. close stimulus and open response). Participants were not instructed to mimic or to avoid mimicry but were only instructed to respond as quickly as possible in all trials. Thus, any differences in reaction time between congruent and incongruent trials (called the "congruency effect", CE) reflect implicit and unconscious mimicry (see a methodology review paper by Heyes, 2011). Response movement direction was orthogonal to stimulus movement direction to avoid spatial compatibility confounds (Press et al., 2008).

There were 6 blocks and 270 trials in total; three blocks required hand-close response and three blocks required hand-open response. Block order alternated and was randomized across participants. Each block presented 36 stimulus trials (where actress' hand opened/closed) and 9 catch trials (where actress' hand kept still) in pseudo-random order. Participants were instructed to refrain from moving their hand in catch trials. Within a block, we adopted a 3×3×3 factorial design in which factors were "direction of first gaze" (AG-1, DG-1 or HG-1), "direction of second gaze" (AG-2, DG-2 or HG-2) and "action congruency" (congruent, incongruent or catch) (Figure 3-1A). Variable delays (200/800ms) were used to prevent anticipatory responses but were not analyzed further.

Similar to Chapter 2, reaction time (RT) was measured by an

electromagnetic device (Polhemus LIBERY system, Colchester, USA). Two sensors were taped on the thumb and middle fingernail of participants' right hand and the sensor's spatial position was recorded at 240Hz. Finger and thumb location data were recorded in Matlab, which also controlled presentation of the video and still image stimuli via the Cogent toolbox. RTs were calculated as the time from the presentation of the 2nd frame of the hand movement video to the time when the participant's hand aperture reached its peak open/close velocity.

3.4 Results

To remove trials in which participants did not attend to the hand stimuli, incorrect responses (0.06%) were excluded from the analysis, as were all RTs smaller than 100ms or greater 800ms (0.07%). To minimize the effect of outliers, we also excluded RTs that were greater than two standard deviations from the conditional means of each participant (0.11%). The CE for each participant was calculated by subtracting RT in congruent trials from RT in incongruent trials.

First of all, in order to compare the mimicry primed by each two-gaze-sequence video, a two-way repeated measures analysis of variance (ANOVA) was conducted on participants' CE with 'first gaze' (AG-1, DG-1 and HG-1) and 'second gaze' (AG-2, DG-2 and HG-2) as variables. The two-way analysis revealed a significant main effect of 'second gaze' on CE ($F_{(2,38)}=26.76$, $p<0.001$). Post hoc t-test showed that participants had a larger CE only when the second gaze was DG-2 (Figure 3-2). However, there was no significant main effect of 'first gaze' ($F_{(2,38)}=0.20$, $p=0.822$) or no significant interaction

between first and second gaze on CE ($F_{(4,76)}$=0.34, p=0.850).

Then we performed a three-way ANOVA on participants' mean RT with 'congruency' (Congruent, Incongruent), 'first gaze' (AG-1, DG-1 and HG-1) and 'second gaze' (AG-2, DG-2 and HG-2) as variables. The three-way ANOVA analysis revealed a significant main effect of 'congruency' ($F_{(1,19)}$=70.92, p<0.001) and 'second gaze' ($F_{(2,38)}$=6.02, p=0.005) on RT. On average, responses were faster for congruent trials (M=309ms, S.E. 14.26) than for incongruent (M=353ms, S.E. 15.83) and responses were faster for DG-2 (M=317ms, S.E. 14.38) than for AG-2 (M=328ms, S.E. 16.00) and HG-2 (M=338ms, S.E. 15.55). Consistent with the main effect of second gaze on CE in two-way ANOVA, the three-way ANOVA showed a significant interaction between congruency and second gaze on RT ($F_{(2,38)}$=26.76, p<0.001). In addition, there was also a significant interaction between first gaze and second gaze on RT ($F_{(4,76)}$=10.90, p<0.001).

To further explore these two interactions, RT data were re-categorized by 'first gaze' or 'second gaze', and were separately analyzed with a two-way ANOVA on the factors of 'congruency' (congruent, incongruent) and 'gaze direction' (AG, DG and HG). The analysis on 'first gaze' data only revealed a significant main effect of congruency ($F_{(1,59)}$=136.69, p<0.001). No other factors reached the significant level (Figure 3-3A), which was in line with the earlier two-way and three-way ANOVA results showing that first gaze did not have impacts on neither CE nor RT. In contrast, the analysis on 'second gaze' data revealed a significant main effect of congruency ($F_{(1,59)}$=124.48, p<0.001) and gaze direction ($F_{(2,118)}$=4.55, p=0.013) (Figure 3-3B). This was also an interaction between congruency and gaze direction ($F_{(2,118)}$=14.90, p<0.001).

Post hoc t-test showed this interaction resulted from a faster congruent movements in DG-2 than in AG-2 ($t_{(59)}$ = 3.27, p<0.002) and HG-2 ($t_{(59)}$ = 4.41, p<0.001).
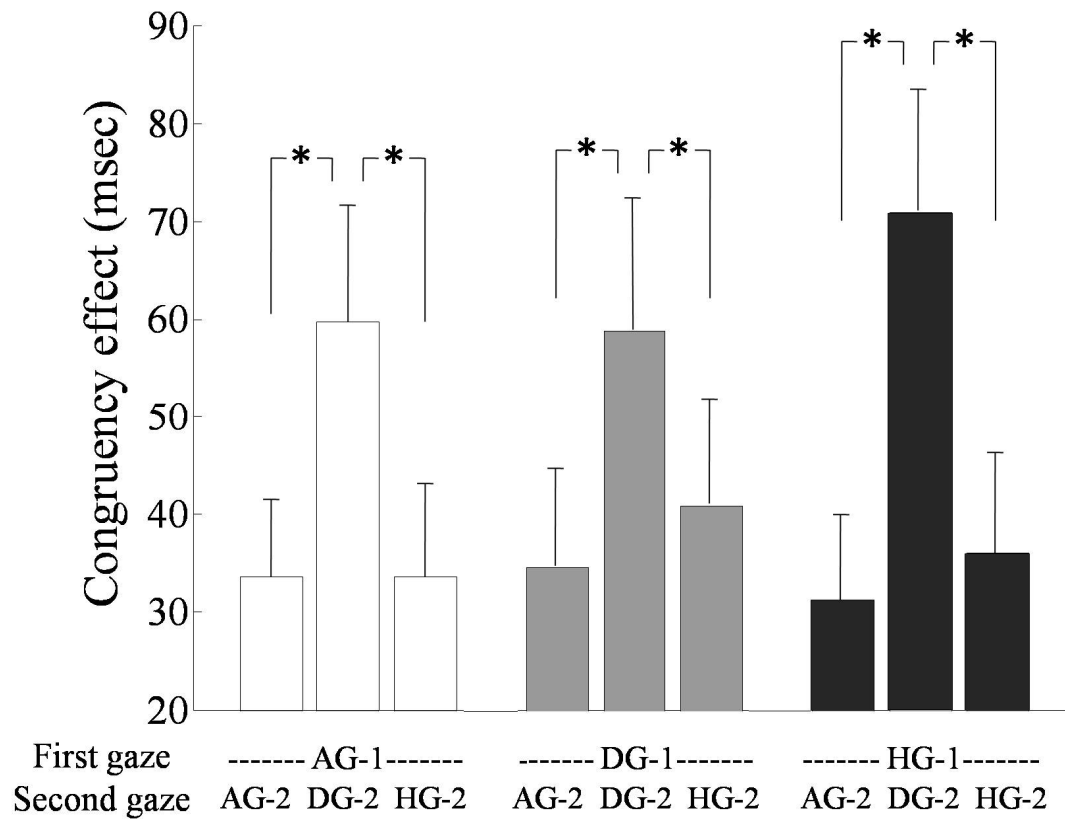
Figure 3-2. Mean congruency effect for each type of the two-gaze-sequence video. Here, CE was enhanced only when the gaze sequence contained DG-2. Asterisk represents the statistically significant difference between two bars. Vertical bars indicate S.E.
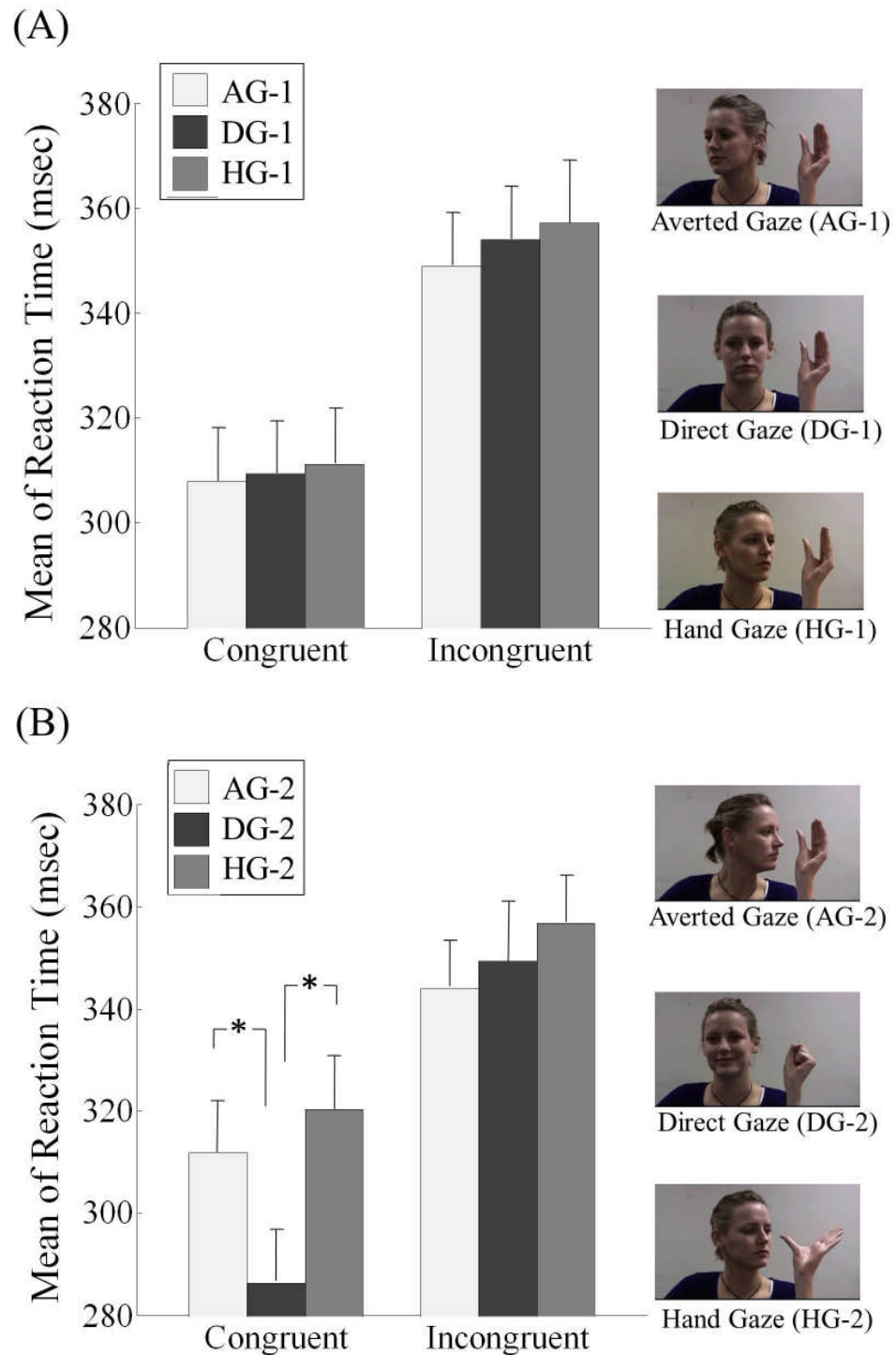
Figure 3-3. Mean reaction time on congruent and incongruent trials for **(A)** first-gaze groups and **(B)** second-gaze groups. Asterisk represents the statistically significant difference between two bars. Vertical bars indicate S.E.

3.5 Discussion

Like Chapter 2 showing that mimicry can be modulated by a single gaze, the current study demonstrated that mimicry is also sensitive to a sequence of two gaze shifts. Specifically, the results revealed that the CE was modulated by the second gaze of the sequence (Figure 3-3B), but was not susceptible to the first gaze (Figure 3-3A). Further analysis on the second gaze suggested that the CE was enhanced only when the second gaze was a direct gaze (DG-2) (Figure 3-2; Figure 3-3B). This was because participants' hand responses to congruent actions were facilitated when preceded by DG-2, but not by AG-2 or HG-2 (Figure 3-3B). These results replicated our previous findings in Chapter 2 that direct gaze enhances mimicry by facilitating responses to congruent trials.

Our findings that mimicry was exclusively enhanced by DG-2 (Figure 3-2) provide compelling evidence that the eye contact effect on mimicry is not driven by the non-social effects of eye gaze. We found that not every gaze sequence including a direct gaze increased mimicry, which rejects the explanation of a general arousal effect. Similarly, the findings that not every gaze sequence with a rightward second gaze enhanced mimicry exclude an explanation of a simple effect of spatial attention. Even in the situations where a strong joint attention effect was implemented by the gaze sequence of DG-1-HG-2, participants did not show any increased mimicry. The only requirement for the eye contact effect on mimicry is that the actress had to look at the participant right before the hand stimuli (DG-2). Thus, we conclude that the eye contact effect on mimicry is not due to any non-social effects of

eye gaze; instead, it is more likely that the social effects of direct gaze drive the enhancement on mimicry.

But what is the specific social effect that underlies the eye contact effect on mimicry? There are possibly two candidates. First, it is possible that the ostensive property of eye contact drives the enhancement of mimicry. Eye contact is a communicative signal that ostensively conveys the sender's communicative intention and interpersonal interest. This ostensive message increases the observer's social engagement and expectation (Senju and Johnson, 2009; Senju and Csibra, 2008) and promotes their social motivation to reciprocate and synchronize (Oberman and Ramachandran, 2007). Several studies suggested that this ostensive property of eye contact increases observer's gaze following, motivation to approach, cooperation and prosocial behaviour (Senju annd Csibra, 2008; Hietanen et al., 2008; Bateson et al., 2006; Haley and Fessler, 2005). According to a recent cognitive model of imitation proposed by Southgate and Hamilton (2008) in which imitation is subject to top-down processes based on analysis of ostensive cues, it is likely that the ostensive-communicative message from DG-2 drives the enhancement of mimicry in the present study.

Strategic monitoring of mimicry by social cues is another mechanism that could mediate the eye contact effect on mimicry. Humans continuously monitor their behaviours to ensure that they are consistent with the current situational context and produce adaptive outcomes. Mimicry has been suggested as an important nonverbal behaviour to facilitate social interaction and enhance liking and affiliation between interaction partners (Chartrand and van Baaren, 2009). However, the prerequisite of this function is that the

copying behaviors have to be somehow perceived by the interaction partner. As eye gaze is a critical attention cue that conveys social knowledge of other's visibility (Birmingham and Kingstone, 2009), we argue that eye gaze could act as a salient signal that strategically monitor when to mimic. This idea of strategic monitoring of mimicry by social signals is compatible with recent studies showing that mimicry is strategically increased when people need to affiliate with others (Lakin et al., 2008). In the present study, the enhancement of mimicry by direct gaze would help people control their mimicry in an economical way and ultimately make their mimicry behavior more efficient and effective. Future research is needed to validate this explanation.

3.6 Conclusion

In sum, the present study used a novel two-gaze-sequence paradigm to dissociate the social and non-social effects of eye gaze on mimicry. We demonstrated that the eye contact effect on mimicry is not based on any arousal or attentional effects, but only driven by the social effects of eye gaze. Future research is needed to clarify the specific social mechanisms underlying this effect.

Chapter 4. The control of mimicry by eye contact is mediated by medial prefrontal cortex

4.1 Abstract

Spontaneous mimicry of other people's action serves an important social function, enhancing affiliation and social interaction. This mimicry can be subtly modulated by different social contexts. Chapter 2 and chapter 3 provide behavioral evidence that direct eye gaze rapidly and specifically enhances mimicry of intransitive hand movements. Based on past findings linking medial prefrontal cortex (mPFC) to both eye contact and the control of mimicry, we hypothesized that mPFC might be the neural origin of this behavioral effect. The present chapter aimed to test this hypothesis. During fMRI scanning, 20 human participants performed a simple mimicry or no mimicry task as previously chapters (the 'hand opening/closing' task), with direct gaze present on half of the trials. As predicted, fMRI results showed that performing the task activated mirror systems while direct gaze and inhibition of the natural tendency to mimic both engaged mPFC. Critically, we found an interaction between mimicry and eye contact in mPFC, superior temporal sulcus (STS) and inferior frontal gyrus (IFG). We then used dynamic causal modeling (DCM) to contrast twelve possible models of information processing in this network. Results supported a model in which eye contact controls mimicry by modulating the connection strength from mPFC to STS. This suggests that mPFC is the originator of the gaze-mimicry interaction and that it modulates

sensory input to the mirror system. Thus, our results demonstrate how different components of the social brain work together to on-line control mimicry according to the social context.

4.2 Introduction

Human behavior depends critically on social contexts, a sensitivity based on a series of rapid and automatic processes such as gaze perception, emotion detection and action mimicry (Adolphs, 2009). However, little is known about the interplay between these processes and how they interact in the brain. In chapter 2 and chapter 3 we demonstrated behavioral evidence that action mimicry can be directly modulated by eye contact: direct gaze rapidly and specifically enhances the mimicry of hand movements compared to averted gaze. The aim of current paper is to use functional magnetic imaging (fMRI) to investigate the neural mechanism of this effect.

Mimicry refers to the unconscious tendency to copy the postures, gestures, and mannerisms of others (Chartrand and van Baaren, 2009). It has been suggested that this spontaneous mimicry acts as a 'social glue' and increases affiliation and liking between interaction partners (Chartrand and van Baaren, 2009). As a form of imitation, mimicry has been strongly associated with the mirror neuron system (MNS) (see 1.2.7). This brain network spans inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) and is engaged in a variety of imitation and imitation learning tasks (Iacoboni et al, 1999; Iacoboni, 2009; Buccino et al., 2004; Rizzolatti and Craighero, 2004). It is claimed that this network implements a "direct-mapping mechanism" that matches an observed action onto a motor representation of that action (Brass

and Heyes, 2005; Rizzolatti and Craighero, 2004).

However, this direct mapping of observed to performed actions is not impervious to other processes, but can be flexibly modulated by higher-level cognitive processes such as intention attribution and social relevance observation (Kilner et al., 2006; Leipelt et al., 2008; Leipelt and Brass, 2010; see 1.2.5). Similarly, studies of mimicry in social contexts also emphasize the importance of controlling when and who to mimic. Attractiveness, friendship and social status can enhance mimicry while social stigma, negative mood and outgroup membership can inhibit mimicry (Chartrand and van Baaren, 2009; see 1.1.5).

One candidate brain system for the control of mimicry by social contexts is medial prefrontal cortex (mPFC). mPFC is considered as a core region for social cognition (Amodio and Frith, 2006). It is engaged when detecting and evaluating direct gaze (Kampe et al., 2003; Kuzmanovic et al., 2009). Brass et al. (2001a, 2005, 2009) suggests that mPFC is engaged when participants must inhibit their natural tendency to mimic, and patient studies suggest damage to prefrontal cortex can lead to over-imitation (Luria, 1980). This evidence makes mPFC a strong candidate for controlling the interaction of gaze and mimicry. Alternatively, the control of mimicry by gaze might be linked to superior temporal sulcus (STS), a key centre for processing of eye gaze (Senju and Johnson, 2009) and a sensory input site to the MNS (Rizzolatti and Craighero, 2004). In the present study, we used our established SRC paradigm to identify brain systems involved in the control of mimicry by eye contact, using both a factorial fMRI event-related design and dynamic causal modeling (DCM).
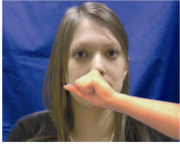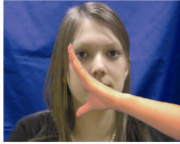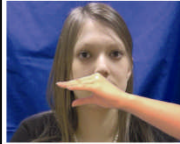
4.3 Materials and methods

Participants

Twenty paid participants (five males, fifteen females; mean age 23, SD= ± 4.8) were recruited for the present study. All participants were right-handed, with normal or corrected-to-normal vision and no history of brain damage. They gave their informed consent to complete the experiment in accord with the local ethics board.

Stimuli and experimental design

In each trial, participants watched a video clip where an actress performed an eye/head movement and a hand movement (Figure 4-1). At the onset of the video clip, the actress was facing away from the camera, with her eyes closed and her left hand still in front of her face. Then she opened her eyes and naturally moved her head either towards the camera which resulted in a direct gaze, or towards her left/right side which resulted in an averted gaze; her hand remained entirely still. Subsequently, the actress performed a hand movement. She either opened her hand or closed her hand (stimulus trials), or remained hand static (catch trials). All stimuli were identical to Experiment 1 in Chapter and were presented with Cogent toolbox running under Matlab 6.5 permitting synchronisation with the scanner and accurate timing of stimuli presentation.

Figure 4-1. Factorial design and example of stimuli. Participants were shown a series of 3s video clips where an actress did a head movement and a hand movement. Only the last frame of each video is illustrated here. Participants were required to make the same pre-specified response (either OPEN or CLOSE hand) in every stimulus trial in a block, as quickly as possible after the actor's hand in video clips began to move. In catch trails where the actress remained her hand still, they had to keep their right hand still but press the scanner button box with their left hand, as soon as they see a small white box appear on the actress' hand. Each movie was defined with respect to the gaze direction and congruency between the hand movement performed by the actress and the participant's pre-specified response. As such, each trial fell into a 2 x 3 factorial design for direct or averted gaze, congruent, incongruent or catch trial.

We used our established SRC paradigm (the 'hand opening/closing' task) to measure mimicry. For each block, participants were required to make the same pre-specified response in every trial. They had to always open or close their right hand as quickly as possible after the actress' hand in video clips began to move. On some trials, the actress' hand opened and on others it closed. Therefore, within a block, the hand movement in the movie was either the same as the pre-specified response (congruent trials, e.g. open stimulus and open response) or the opposite of the pre-specified response

(incongruent trials, e.g. close stimulus and open response). Past studies have found a clear congruency effect (CE) in this paradigm and took CE as a reliable measure of mimicry, with faster responses on congruent trials which were facilitated by mimicry of observed congruent action and slower responses on incongruent trials where participants must inhibit the natural tendency to mimic the actress's hand action (Heyes, 2011; Heyes et al., 2005; Press et al., 2008). Our previous studies demonstrated that this CE can be enhanced by eye contact where direct gaze significantly reduces reaction times on congruent trials (see Chapter 2 and Chapter 3). Compliance with the hand movement task was monitored from the scanner control room. For technical reasons, it was not possible to measure precise reaction times during fMRI, but as the behavioral result has now been replicated four times in different participant groups (Chapter 2, Experiment 1 and Experiment 2, and two pilot studies), we are confident that it is robust.

To prevent anticipatory responding, there was a variable delay (200 or 800ms) between the end of the actress' head movement and start of her hand movement in the video and in addition, approximately 20% of trials in a block were catch trials. In catch trials the hand observed in the video remained static. Participants were instructed to refrain from moving their right hand, but were asked to detect a small white box that appeared on the top of the still hand and press a response button with their left hand when the white box was detected. Thus, participants mimicked the actress' hand movements only in stimulus trials (congruent and incongruent), but not in catch trials. Participants were trained on all tasks (congruent, incongruent, catch) for approximately 5 minutes prior to the fMRI measurement.

We adopted a 2 x 3 factorial event-related design in which the factors were "Gaze Direction" (two levels: direct or averted gaze) and "Action Congruency" (three levels: congruent or incongruent or catch trials) (Figure.4-1). Each trial was defined by these two factors as direct gaze with congruent action (*Direct-Cong*), direct gaze with incongruent action (*Direct-Incong*), direct gaze with catch action (*Direct-Catch*), averted gaze with congruent action (*Averted-Cong*), averted gaze with incongruent action (*Averted-Incong*) and averted gaze with catch action (*Averted-Catch*). There were 6 blocks; three blocks required a hand-close response and three blocks required a hand-open response. Block order alternated and was randomized across participants. Each block presented in a pseudorandom order, 32 stimulus trials (16 congruent and 16 incongruent) and 9 catch trials. The first trial in each block was always a catch trial and was excluded from further analysis.

fMRI Data Acquisition

Subjects lay supine on the scanner bed, with their right hand uprightly positioned on the abdomen and left hand positioned over the fMRI button box. Participants' right hand was carefully stabilized, and form-fitting cushions were used to prevent arm, hand, and head motion. To attenuate scanner noise, participants were provided with earplugs.

Imaging was performed using a 3T Phillips Achieva scanner, equipped with an 8 channel-phased array head coil. 38 axial slices (field of view: 240 x 240 mm^2, matrix: 80 x 80; thickness: 3 mm) parallel to bicommissural line (AC-PC) were acquired using a T2*-weighted gradient echo planar imaging (EPI) sequence (TR: 2500 ms; TE: 40ms; flip angle: 80°). Prior to the functional runs, structure images were also required for each participant using

high-resolution T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence.

Conventional General Linear Model (GLM) Analysis

To remove sources of noise and artifact, functional data were realigned, unwarped, corrected for slice timing, normalized to the MNI template with a resolution of 3mm x 3mm x 3mm and spatially smoothed (8mm) using SPM8 software. A design matrix was fitted for each subject with one regressor for each movie type (*Direct-Cong, Direct-Incong, Direct-Catch, Averted-Cong, Averted-Incong and Averted-Catch*) and combined across the six blocks. Each movie was modeled as a boxcar with the duration of that movie convolved with the standard hemodynamic response function. In order to reduce the influence of reaction time variability between conditions on the GLM analysis (Grinband et al., 2008), we added an extra column in the design matrix, modeling our previous average reaction time scores (Chapter 2, Experiment 1) in each condition as a parametric regressor.

In order to localize brain regions engaged in the hand movement task, two contrasts [*Congruent trials > Catch trials*], [*Incongruent trials > Catch trials*] were calculated across all movies. To localize brain regions for inhibition of mimicry, a contrast for the main effect of mimicry inhibition [*Incongruent trials > Congruent trials*] was calculated. Two contrasts for the simple effect of the inhibition of mimicry were also calculated, [*Direct-Incong > Direct-cong*], [*Averted-incong > Averted-cong*]. To identify brain regions that code the eye contact effect, a contrast for the main effect of eye contact [*Direct > Averted*] was performed across all movies. Also, two contrasts for the simple effect of eye contact were calculated across all movies of stimulus trials, [*Direct-Cong*

> *Averted-Cong*] and [*Direct-Incong* > *Averted-Incong*]. Finally, we calculated the interaction between mimicry and eye contact, both as [(*Direct-Cong* > *Direct-Incong*) > (*Averted-Cong* > *Averted-Incong*)] and as the inverse contrast [(*Direct-Incong* > *Direct-Cong*) > (*Averted-Incong* > *Averted-Cong*)]. Contrast images for all participants were then taken to the second level for a random-effects analysis in SPM8. Brain regions were initially thresholded at a voxel-level threshold of p < 0.001 and 30 voxels. Only regions that survive a cluster-level FWE correction of p < 0.05 over the whole brain are discussed and reported in Table 4-1 and Figure 4-2.

Dynamic Causal Modeling (DCM)

To explore information processing between brain areas under different experimental manipulations, we performed an effective connectivity analysis using DCM10 (Friston et al. 2003). DCM treats the brain as a dynamic input-state-output system. The inputs correspond to experimental manipulations. The state variables are neuronal activities (firing rates), and the outputs are the regional hemodynamic responses measured with fMRI. The idea is to model changes in the hidden states and effective connectivity, which cannot be observed by fMRI directly, using the known inputs and outputs. Three kinds of coupling parameters are estimated in DCM: 1) direct, extrinsic inputs to the system (i.e., the direct effect of eye contact on mPFC); 2) 'intrinsic' or 'fixed' connections that couple neuronal states between regions (i.e., the connectivity strength from mPFC to STS); and 3) modulatory parameters that model the changes in fixed connectivity induced by the experimental manipulations (i.e., the additive change a certain manipulation, like direct gaze, has on the strength of a connection).

For each participant, models were constructed to define the connections between and the inputs to three regions identified in the mimicry-gaze interaction contrast (Figure 4-2d). These were (1) the left STS as the 'sensory input' of MNS (x=-48, y=-19, z=-2, coordinates are from Table 1), (2) the right IFG as the 'motor output' of MNS (x=45, y=26, z=-17), (3) the right mPFC as a potential control region (x=6, y=44, z=34). Input data to the models was extracted in a participant-specific manner from each of these three regions (Figure 4-3a). In detail, the region-specific time series (concatenated over the six blocks) comprised the first eigenvariate of all voxels within a 5-mm-radius sphere centered on the subject-specific peak in the interaction contrast. The subject-specific peak was constrained within a 15-mm-radius sphere centered on the peak coordinates from the group random-effect analysis (Figure 4-3a). Of the twenty participants, we could not identify an individual peak in the STS in one participant, in the IFG in one participant and in the mPFC in one participant. Thus, the data from these three participants were excluded from the DCM analysis, leaving 17 participants in this analysis.

The three regions in each model were set to be bidirectionally connected, according to anatomical evidence from human and monkey (Figure 4-3b). For simplicity (Stephan et al., 2010), a new design matrix was created for DCM analysis which modeled two critical factors: (1) the hand movement task (stimulus trials vs catch trials) and (2) the Interaction of gaze and mimicry ([*Direct-Cong > Direct-Incong*] vs [*Averted-Cong > Averted-Incong*]) as parametric factors on the individual trials. This allows us to consider only these two factors as extrinsic inputs in the current study, and substantially simplifies our original 2x3 factorial design. Holding the number of parameters

constant for the intrinsic connectivity structure, extrinsic inputs and modulatory effects, we compared 12=2x3x2 models in order to address three central questions (Figure 4-3d): (1) is the eye contact effect on mimicry due to top-down modulation from mPFC (model 1-6) or bottom-up gating from STS (model 7-12)? ; (2) how does the interaction of gaze and mimicry modulate processing within the network? Is it by modulating the connection strength between mPFC and STS (models 1, 4, 7, 10) or by modulating the connection strength from mPFC to IFG (models 2, 5, 8, 11) or by modulating the connection strength from STS to IFG (models 3, 6, 9, 12)?; (3) whether the hand movement task affects the connection strength from STS to IFG (models 4, 5, 6, 10, 11, 12) or not (models 1, 2, 3, 7, 8, 9)?
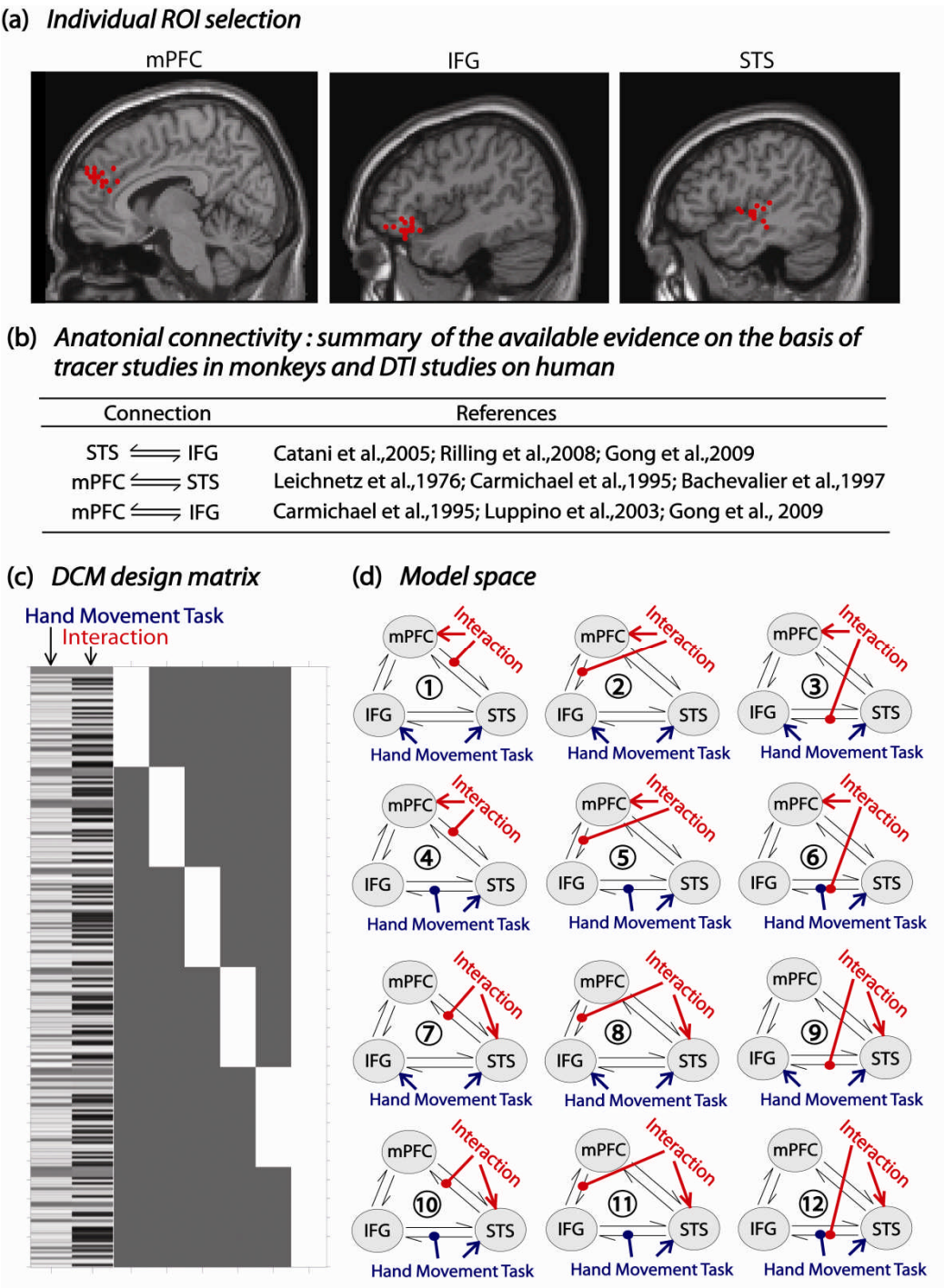
Figure 4-3. DCM inputs. (a) Region selection and time series extraction from 17 subjects. Each red point indicates the centre of the 5mm radius sphere where data was extracted for one participant. (b) Anatomical criteria used to define the intrinsic connectivity structure. (c) The matrix design for DCM. Only two critical factors were analyzed in DCM: hand movement task and Interaction (d) Model space of all 12 models considered in the DCM analysis.

Bayesian models Selection (BMS)

To determine the most likely of the 12 models given the observed data from all subjects, we implemented a fixed-effects (FFX) and a random-effects (RFX) group analysis (Stephan et al., 2009). In the FFX case, one assumes that the optimal model is identical across the population. It uses group log-evidence to quantify the relative goodness of models, which is the exponentiated sum of the log model evidences of each subject-specific model (Penny et al., 2004). As the log evidence of each subject-specific model estimated by FFX group analysis depends not only on model fit but also model complexity, we limited ourselves to the 12 models that were equated for the number of parameters. Usually, a difference in group log-evidence of three is taken as statistically strong evidence (Kass and Raftery, 1995). Thus if the group log-evidence of one model is bigger than the other models' by three or more, that model would be considered by FFX analysis as the optimal model (Stephan et al., 2010).

Because the FFX analysis is vulnerable to outlier subjects, we also implemented a RFX analysis which accounts for heterogeneity of model structure across subjects (Stephan et al., 2009). It uses hierarchical Bayesian modeling that estimates the parameters of a Dirichlet distribution over the probabilities of all models considered. These probabilities define a multinomial distribution over model space enabling the computation of the posterior probability of each model given the data of all subjects and the models considered. The results of RFX analysis are reported in terms of the exceedance probability that one model is more likely than any other model. The optimal model in RFX analysis would be considered as the one with the

largest exceedance probability as well as above chance-level.

For the optimal model(s) selected by FFX and RFX analysis, the model parameters (intrinsic connection strength, effects of extrinsic inputs and modulatory effects of extrinsic inputs on connection strength) were entered into *t* tests at the group level. This allowed us to summarize the consistent findings from the subject-specific models using classical statistics.

4.4 Results

Neural correlates of the hand movement task

The two contrasts *Congruent trials > Catch trials, Incongruent trials > Catch trials* both yielded strong activations in primary motor cortex, cerebellum, IFG and temporal pole/middle temporal gyrus (MTG). Activations also extended to large areas in parietal and temporal lobe (Table 4-1 and Figure 4-2a).

Neural correlates of inhibition of mimicry

We examined brain regions engaged when participants must inhibit their natural tendency to mimic the observed hand action (*Incongruent > Congruent*). Regardless of gaze direction, this main effect revealed greater activation in two regions: IPL and cuneus. We further examined the simple effect of the inhibition of mimicry in either direct or averted gaze conditions. Specifically, when mimicry was preceded by an averted gaze, brain areas that showed greater response to 'incongruent' trials than 'congruent' trials (the contrast *Averted-Incong > Averted-Cong*) included mPFC, temporal-parietal junction (TPJ), middle occipital gyrus, MTG/STS, IFG, middle frontal gyrus (MFG), IPL, cingulated and precuneus (Table 4-1 and Figure 4-2b). This result

replicates the findings from Brass et al. (2001a, 2005, 2009) that mPFC and TPJ have a role in inhibition of mimicry. However, no region was found to show greater activation to 'incongruent' trials than 'congruent' trials in direct gaze conditions (the contrast *Direct-Incong > Direct-Cong*).

Neural correlates of the eye contact effect

We examined the brain regions responsive to direct gaze compared to averted gaze (Main effect, *Direct > Averted*). No regions survived our thresholds in this contrast. We then separately examined the simple effect of eye contact in either congruent or incongruent conditions. The contrast *Direct-Cong > Averted-Cong* revealed increased neural activity in MTG/STS, IPL and mPFC (Table 4-1 and Figure 4-2c). This result replicates the findings from Kampe et al. (2003) that mPFC is engaged by eye contact. No brain region was found in the other contrast *Direct-Incong > Averted-Incong.*

Neural correlates of interaction between mimicry and eye contact

Results from the interaction contrast [(*Direct-Cong > Direct-Incong*) > (*Averted-Cong > Averted-Incong*)]*)* revealed activity in three areas: the mPFC, IFG and STS (Table 4-1, Figure 4-2d). Illustrative plots of the parameter estimates in mPFC revealed that the interaction contrast was mainly driven by the strong engagement of mPFC in the *Direct-congruent* and *Averted-Incongruent* conditions and weak engagement of mPFC in Averted-congruent condition (Figure 4-4c). Further plots of the relationship between this interaction contrast and the simple effect of eye contact and the simple effect of the control of mimicry revealed that all three contrasts overlapped in mPFC (Figure 4-4a). The inverse contrast [(*Direct-Incong > Direct-Cong*) > (*Averted-Incong > Averted-Cong*)] did not yield any significant clusters.

Table 4-1. Cortical activation for the hand movement task, inhibition of mimicry, eye contact effect and the gaze-mimicry interaction.

Region	Number of voxels	T	P cluster corrected (FWE)	MNI coordinates		
				x	y	z
Hand movement task						
Congruent > Catch						
Primary motor cortex and Cerebellum, extended to	179884	19.07	< 0.001	-39	-19	55
				21	-52	-29
whole parietal and temporal lobe				-24	-10	1
Inferior frontal gyrus	150	10.82	< 0.001	-42	32	-20
				-48	26	-11
				-45	38	1
Temporal pole/ Middle temporal gyrus	82	6.32	0.006	51	11	-38
Fusiform gyrus	75	4.08	0.038	-45	-40	-26
Incongruent > Catch						
Cerebellum and Primary motor cortex, extended to	215881	21.23	< 0.001	15	-52	-26
				24	-52	-32
whole parietal and temporal lobe				-39	-19	55
Inferior frontal gyrus	79	10.13	0.003	-54	23	13
Temporal pole/	65	5.00	0.034	51	8	-41
Middle temporal gyrus				45	14	-44
Inhibition of Mimicry						
Main effect: Incongruent > congruent						
Inferior parietal lobe	137	5.22	< 0.001	-54	-25	46
				-45	-31	37
				-30	-25	55
Cuneus	96	3.88	0.037	6	-76	10
				-3	-94	10
				9	-88	19
Simple Effect: Averted-incong > averted-cong						
Medial prefrontal cortex	753	8.83	< 0.001	9	44	31
				9	41	22
				15	53	22
Temporal-parietal junction	121	7.64	< 0.001	63	-49	28
				57	-46	13
				63	-46	37
Middle occipital gyrus	451	6.77	< 0.001	18	-100	16
				3	-79	10
				-9	-79	7
Middle temporal gyrus	138	6.34	0.002	-36	-31	10

Region						
and Superior temporal sulcus				-51	-25	-5
				-42	-31	-8
Temporal pole	112	5.96	0.005	-45	11	-14
				-54	5	-2
Inferior frontal gyrus	113	5.40	< 0.001	42	20	-8
				39	23	4
Cingulate and Precuneus	204	5.30	< 0.001	-9	-22	43
				0	-19	46
				21	-34	49
Middle frontal gyrus	96	5.29	0.005	24	20	49
				30	23	58
Cerebellum and Thalamus	288	5.11	< 0.001	6	-16	4
				24	-22	4
				-6	-16	-2
Primary motor cortex and Inferior parietal lobe	60	4.86	0.020	-39	-25	40
				-48	-25	40
				-39	-28	28
Cuneus	155	4.44	<0.001	6	-79	37
				6	-79	49
				-6	-70	46
Superior parietal lobe	61	3.82	0.048	0	-49	58
				-3	-49	49

Eye contact effect:
Simple Effect: Direct-cong > averted-cong

Region						
Medial prefrontal cortex	45	7.37	< 0.001	9	-10	1
	47	5.64	< 0.001	15	44	13
Superior temporal sulcus/ Middle temporal gyrus	77	7.19	< 0.001	48	-46	1
				48	-40	-5
				51	-31	-11
Inferior parietal lobe	84	6.70	< 0.001	51	-46	49
				54	-49	49
				45	-70	40

Interaction
(Direct-Cong > Direct-Incong) > (Averted-Cong > Averted-Incong)

Region						
Superior temporal sulcus	53	7.12	< 0.001	-48	-19	-2
				-51	-28	-2
				-57	-34	4
Medial prefrontal cortex	128	6.76	< 0.001	6	44	34
				15	44	16
Inferior frontal gyrus	94	6.22	< 0.001	45	26	-17
				39	26	-23
				24	14	-26

Note. Only regions surviving a whole-brain voxel-level threshold of p<0.001 and a FWE cluster-corrected level threshold of *p*<0.05 are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed.
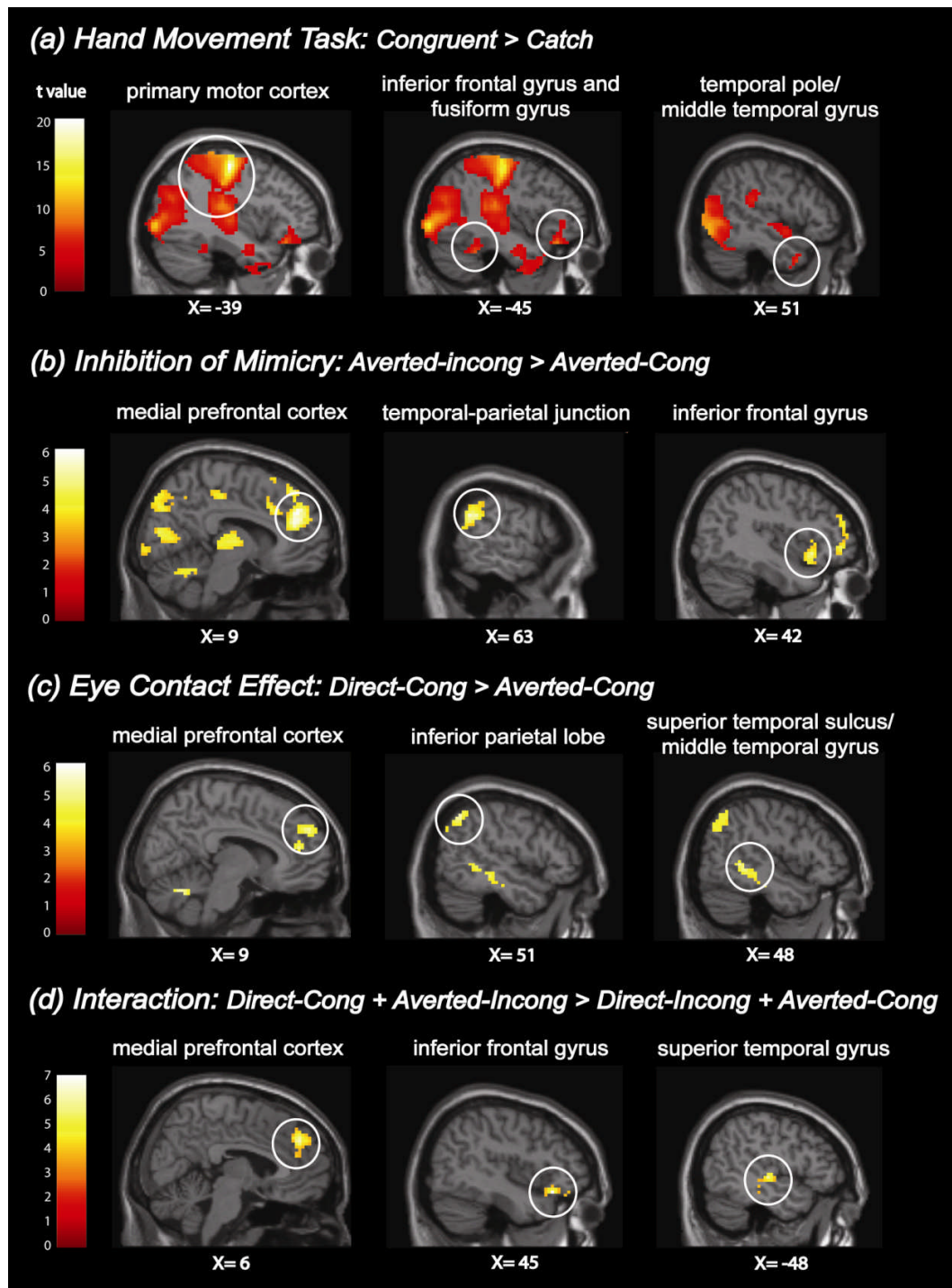
Figure 4-2. Bain regions showing increased activations for (a) the hand movement task, (b) the simple effect of inhibition of mimicry, (c) the simple effect of eye contact, (d) the interaction of gaze and mimicry. Coordinates are listed in Table 1.
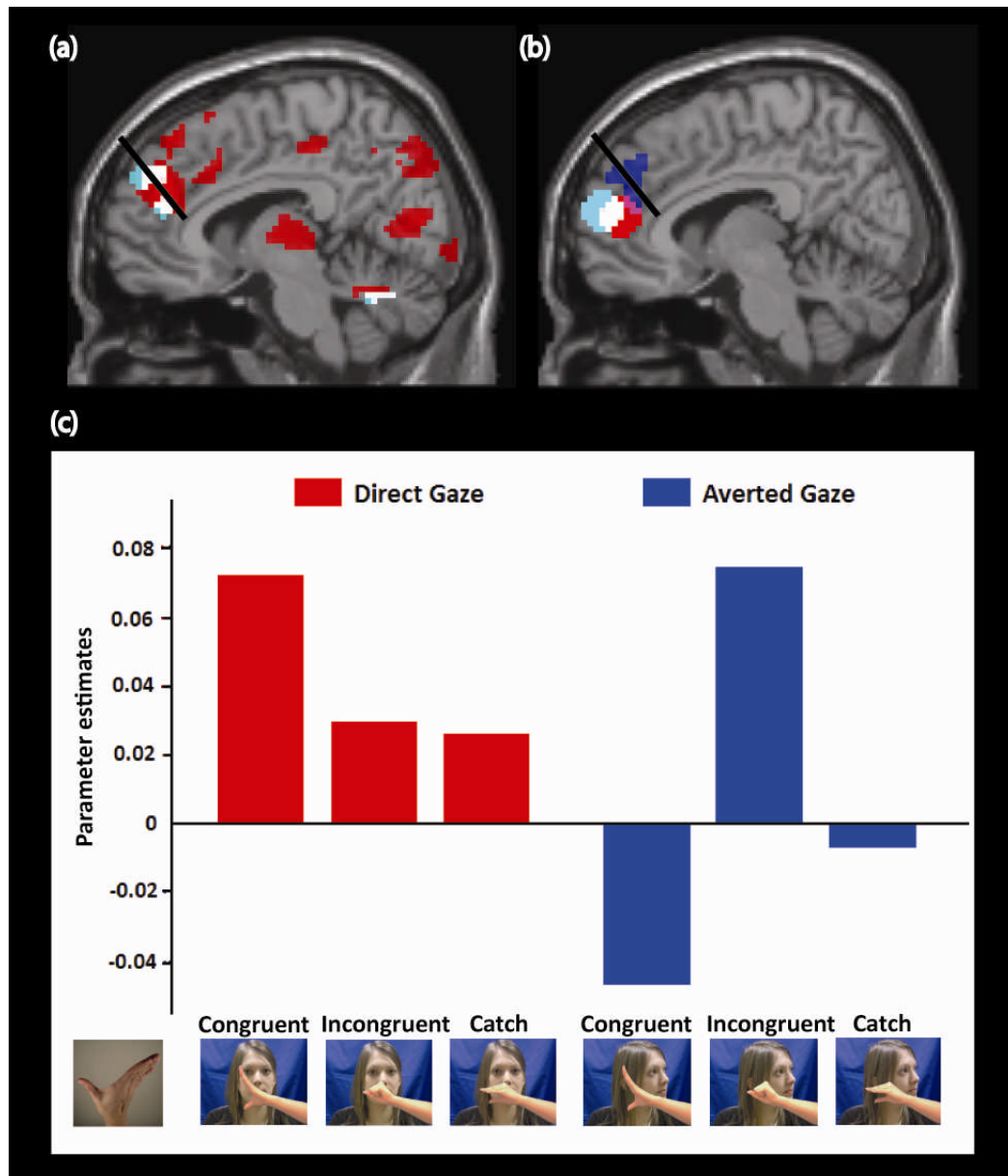
Figure 4-4. Activations in mPFC. (a) Mapping of activations of the inhibition of mimicry and the eye contact effect in current study. Areas with red color represent the simple effect of the inhibition of mimicry. Areas with cyan color represent the simple effect of eye contact. White region is the overlap of the two activations. Bold black line represents the functional border between posterior and anterior mPFC in Amodio and Frith' s (2006) review paper (b) Comparisons of mPFC activation for the mimicry-gaze interaction between current study and two related studies. Blue region represents the mPFC activation for interaction in current study. Red region represents the mPFC activation for the eye contact effect in Kampe et al., (2003). Cyan

region represents the mPFC activation for the inhibition of mimicry in Brass et al., (2001). White region was the overlap of the two past studies. (c) Parameter estimates (SPM betas) for mPFC activations emerged from the interaction contrast in each experimental condition.

DCM and BMS results

Figure 4-5a (right) shows the relative group log-evidences across the 12 models and the structure of the best model (model 4). The relative group log-evidences refer to log-evidences summed over 17 subjects for 12 models relative to the worst model. The FFX group analysis provided strong evidence for model 4, as the difference of the relative group log-evidence between model 4 and the second best model (model 10) was 3.52. The RFX analysis on the same set of models gave a compatible result, with model 4 providing the best description of the observed data. As shown in Figure 4-5b (right), model4 was associated with the largest model exceedance probability of 0.195, which is much more than the exceedance probability of 1/12=0.083 when assuming a uniform distribution over models. As the exceedance probability of a particular model in the RFX analysis does not only depend on the data but also the set of models tested, we also directly compared the top two models 4 and 10 in RFX analysis. Again BMS revealed a high exceedance probability favoring model 4 relative to model 10 of 0.96.

(a) *The optimal DCM : Fixed-effects analysis (FFX)*
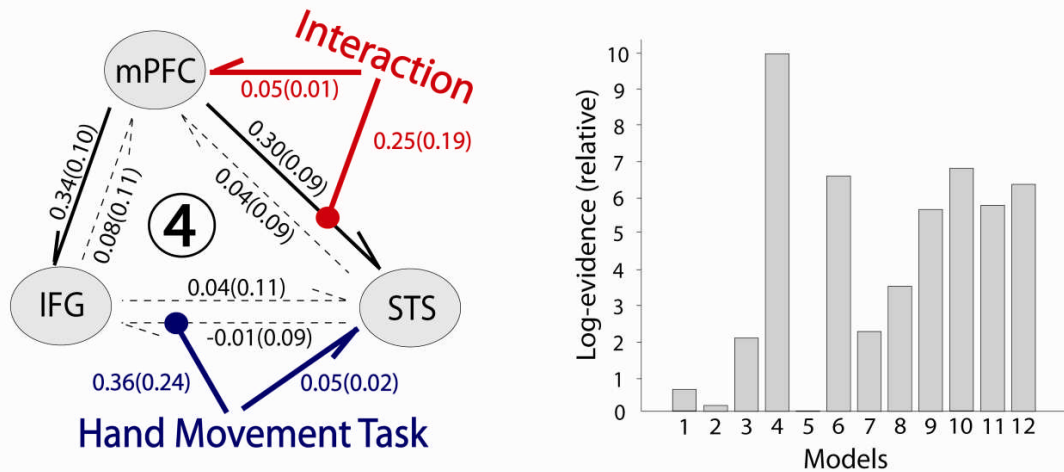
(b) *The optimal DCM : Random-effects analysis (RFX)*
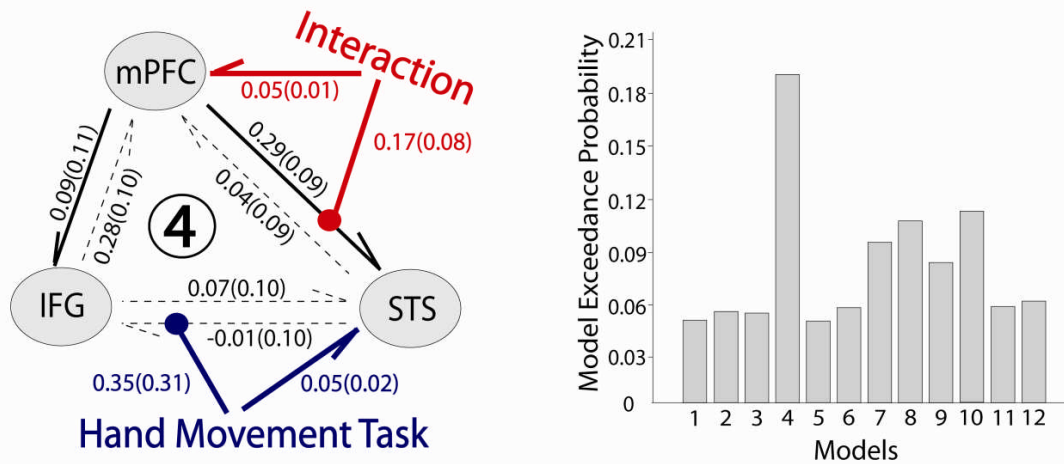
Figure 4-5. The optimal model selected by the FFX analysis (a) and RFX analysis (b). The Left graph in each analysis showed the parameters for the optimal model, no 4. Values are the across-subjects mean (SD) of rate constants for intrinsic connections, direct effects of extrinsic inputs and modulatory effects on a certain connection, estimated by DCM10 ($p < 0.05$ in t-test indicated by solid lines). The right graph in each analysis showed the results of Bayesian model selection. The relative group model evidence (a) and model exceedance probability (b) is the highest for model 4.

The left column in Figure 4-5 illustrates model 4 with the parameter estimates from the FFX and RFX analyses. In this top-down modulation model,

the interaction conditions engage mPFC and enhance the connection from mPFC to STS, while hand movement task engages STS and significantly enhances the connection from STS to IFG. As all 12 models were equated for the parameter number of extrinsic inputs, intrinsic connectivity structure and modulatory effects, the difference in model evidence is only due to model fit and not model complexity. The magnitude of these effects can be seen in the rate constants given on each arrow (numbers in brackets are standard deviation). The rate constant refers to the rate of change of neuronal activity (hertz) in one area as induced by another area or by an extrinsic input. For intrinsic connections, only the rate constants of two connections, mPFC → STS and mPFC → IFG, were significantly different from zero (t_{17}=8.20, p<0.001 and t_{17}=6.29, p<0.001, respectively). Figure 4-5 also shows the average rate constants in mPFC induced by interaction (red line) and the average rate constants in STS induced by hand movement task (blue line). Consistent with conventional GLM analysis, the rate of the neuronal activity in mPFC was significantly enhanced by 0.05 Hertz in interaction conditions and the neuronal activity in STS was significantly increased by 0.05 Hertz when subjects performed the hand movement task. Moreover, Figure 4-5 shows the average rate constants for the modulatory effects on the intrinsic connections by the interaction and the task. When eye contact interacts with mimicry, the average rate constant of the connection strength from mPFC to STS significantly increased from 0.30 to 0.55 in FFX analysis and from 0.29 to 0.46 in RFX analysis (note that the rate constants for intrinsic connection and modulatory effects are additive, thus 0.30+0.25=0.55 in FFX analysis or 0.29+0.17=0.46 in RFX analysis). When subjects were engaged in the hand

movement task, the connection from STS to IFG had a significant increase in rate constants from near zero to 0.34-0.35. These parameters for the optimal model highlight three important features of our data: First, the two significant intrinsic connections from mPFC to STS and from mPFC to IFG suggest that mPFC persistently modulates activity of IFG and STS, regardless of task or stimuli. Second, the hand movement task involves more information propagation between different parts of MNS, especially the connection from sensory input part (STS) to motoric part (IFG). Third, the interaction conditions directly influenced mPFC and enhanced the connection strength from mPFC to STS. This supports our hypothesis that mPFC has a central role in the control of mimicry by eye contact, and demonstrates that this control is implemented at the input stage of the MNS (STS) rather than at the motor output (IFG).

4.5 Discussion

Our study aimed to reveal the brain systems underlying the control of mimicry by eye contact. The results were compatible with previous findings on the role of the MNS in imitation tasks and the role of mPFC in the inhibition of mimicry and eye contact effect. More importantly, we revealed an interaction between mimicry and eye contact in mPFC, STS and IFG, suggesting these three regions are critical in the control of mimicry by eye contact. The subsequent DCM analysis supports a model in which mPFC is the origin of this control and the connection strength between mPFC and STS was increased during the interaction. We consider the implications of these results for social cognition.

Mimicry, the eye contact effect and the inhibition of mimicry

In accordance with a meta-analysis on action and imitation tasks (van Overwalle and Kaeten, 2009), we report strong activations in IFG, parietal and temporal regions including IPL and STS when participants performed the hand movement task. In addition, we found the connection strength from STS to IFG was significantly enhanced by the hand movement task, which supports the crucial role of these two regions in the basic sensory-motor mapping process.

Our results are consistent with previous studies of gaze processing. When participants were engaged in congruent hand movements, a clear eye contact effect emerged in mPFC, STS, and IPL. Activation of mPFC and STS by direct gaze is consistent with previous fMRI studies in humans (Kampe et al., 2003; Nummenmaa and Calder, 2009; Senju and Johnson, 2009) and single-cell recordings in monkeys (Perrett et al., 1992; Emery, 2000), which together suggest that STS and mPFC are important for gaze processing. However, just as the behavioral results in Chapter 2 showed that reaction time in incongruent trials did not change by gaze conditions, the current fMRI data demonstrated that no brain regions showed more activation to direct gaze than averted gaze in incongruent trials.

Our results are also in line with previous studies of the inhibition of mimicry. In averted gaze conditions, trials requiring inhibition of mimicry engaged portions of the frontal lobe (mPFC, IFG, MFG) and TPJ. This pattern of activation resembles that previously reported by other researchers (Brass et al., 2001a, 2005, 2009) in which they used a different stimulus-response compatibility paradigm to study the inhibition of mimicry. Frontal lobe activity

during inhibitory processes is also supported by early clinical findings that inhibition of inappropriate responses (e.g. incongruent trials) is a function performed in the frontal lobe (Luria, 1980; Vendrell, 1995). However, it is important to note that these frontal brain regions only showed greater activations to incongruent trials in averted gaze conditions, but not in direct gaze conditions. In particular, Figure 4-4c shows that mPFC is activated in all three direct gaze conditions (direct-congruent, direct-incongruent and direct-catch), with no reliable differences between them. In our paradigm, gaze information was available near the start of the trial whilst the type of mimicry was not apparent until near the end of the trial. Consequently, we suggest that in direct gaze conditions, strong BOLD signal in mPFC elicited by eye contact dominates the later BOLD signal elicited by the inhibition of mimicry in incongruent trials.

Moreover, it is interesting to see that mPFC regions engaged by the inhibition of mimicry and by eye contact overlap (Figure 4-4a). These results support Brass and colleagues' claim that inhibition of mimicry overlaps with higher level social-cognitive abilities both at the functional and the neural level (Brass et al., 2009). By asking participants to complete a mimicry-inhibition task, a mentalizing task and a paradigm assessing self-referential judgments, Spengler et al. (2010a) found an overlap of activated brain regions in mPFC between the mimicry-inhibition task and the other two social cognition tasks. They also used neuropsychological evidence from patients with prefrontal and temporo-parietal lesions to show that the inhibition of mimicry is functionally linked to aspects of social cognitive processing. Here, we found another social cognitive ability—gaze processing—anatomically overlapping with the

inhibition of mimicry. Future studies can explore whether gaze processing and the inhibition of mimicry are functionally linked in patients with prefrontal lesions.

The role of mPFC in the control of mimicry by eye contact

The critical analysis in the present study was of the interaction between mimicry and eye contact. Our previous study demonstrated a behavioral interaction, with direct gaze enhancing mimicry (Chapter 2 and Chapter 3). Here, our fMRI analysis showed the engagement of mPFC, STS and IFG in this interaction, which is consistent with our hypothesis that mPFC is a key mediator in how eye contact modulates mimicry. To distinguish the roles of mPFC, STS and IFG in this interaction, we used a DCM approach that tests the functional connectivity of these regions. The DCM analysis revealed a best-fitting model in which the interaction of mimicry and eye contact activates mPFC and alters the connection strength from mPFC to STS. This suggests that mPFC is the originator of the eye contact effect, and this region modulates sensory processes in STS which in turn impacts on IFG. In cognitive terms, mPFC seems to impose top-down control on how actions are processed in STS and IFG.

Inspection of the parameter estimates in mPFC (Figure 4-4) provides hints about the underlying mechanisms. Direct-congruent and averted-incongruent trials are two orthogonal conditions that are believed to have distinct cognitive processes. Strong activation of mPFC in these two conditions (Figure 4-4c) suggests that they both demand a strong level of top-down control, with inhibition in the case of the averted-incongruent trials and enhancement in the case of direct-congruent trials. This interpretation

assumes that the BOLD signal does not distinguish inhibition from enhancement but just reflects the overall amount of control. This is also evident in the other conditions, where averted-congruent and averted-catch have the lowest mPFC signal, because these two conditions require neither enhancement nor inhibition. The DCM analysis revealed that in the interaction contrast [(*Direct-Cong* > *Direct-Incong*) > (*Averted-Cong* > *Averted-Incong*)] connectivity from mPFC to STS is increased, which suggests that the same pattern of enhancement and inhibition acts on STS. Unfortunately, the DCM design does not permit a simple-effect analysis to confirm this (Stephan et al., 2010). The suggestion that mPFC can both enhance and inhibit mimicry takes our results beyond previous research (Brass et al.,2001a) which emphasized only an inhibitory role for mPFC.

The precise anatomical location of the mPFC cluster supports this possibility that this cluster contains distinct neuronal populations with excitatory and inhibitory roles (Figure 4-4a). A meta-analysis of task-related neural activations in mPFC revealed three functional divisions within this region (Amodio and Frith, 2006). The posterior region of mPFC is activated in response inhibition tasks; the anterior region is responsible for facilitating social cognition tasks involving mentalising; the orbital region has been linked to the punishment or reward monitoring. When the location of the mPFC cluster in our data was mapped onto these three functional divisions, we found that it was just at the boundary between posterior and anterior mPFC (Figure 4-4a). It was more dorsal than other studies simply testing the inhibition of mimicry (Brass et al., 2001a) or the eye contact effect (Kampe et al., 2003) (Figure 4-4b). As the posterior region involves response inhibition

and the anterior region is responsible for facilitating the performance in social cognition tasks, the boundary location supports the possibility that this region of mPFC can both enhance and inhibit mimicry in different contexts. Further studies will be needed to clarify how control signals originating from different neuronal populations within mPFC related to both BOLD signal and reaction time measures.

Broader Implications

In a broader cognitive framework, our findings support current theories suggesting that mimicry in social contexts requires brain systems beyond the MNS (Southgate and Hamilton, 2008; Brass, et al, 2009). In particular, it has been suggested that basic imitation mechanisms implemented in the MNS must be subtly controlled by other social cues (Southgate and Hamilton, 2008). These social cues could act either on the input to the MNS or on the outputs from the MNS (Heyes, 2011). Previous studies of the inhibition of mimicry (Brass et al, 2005, 2009) showed that mPFC mediates modulation to the output of the MNS. Our DCM analysis complements these findings and shows that under different social gazes, mPFC enhances mimicry by modulating an input to the MNS. More specifically, MNS input is modulated via changing the connection strength from mPFC to STS. Thus, these data are compatible with Heyes' model which suggests mimicry can be modulated by changing either input to or output from the MNS but not changing the sensorimotor mapping itself (Heyes, 2011).

Moreover, numerous behavioural studies suggest that imitation is flexible and can be influenced by higher level cognitive and affective processes, such as mindsets (van Baaren et al., 2009), social status (Cheng and Chartrand,

2003), social attitude (Leighton et al., 2010), strategy (Rumiati et al, 2009), intentionality (Massen and Prinz, 2009), rationality (Gergely et al., 2002) and eye contact (Chapter 2 and Chapter 3). Several of these processes have previously been linked to mPFC, including responses to social status (Zink et al., 2008), rationality (Brass et al., 2007) and eye contact (Kampe et al., 2003). Our study is the first to investigate the relationship between social sensitivity in mPFC and the control of imitation, and specifically demonstrated that mPFC controls mimicry online by modulating the sensory input of the MNS. In the future, it will be interesting to test whether other higher level social cognitive processes modulate mimicry through the mediation of mPFC and how mPFC influences the input or output of the MNS.

The present study focused on eye contact because this is a rapidly processed social cue (Senju and Johnson, 2009). Detection of eye contact may be one way to initialize a communication and begin focusing on another person's mental state (Kampe et al., 2003). Our data provide initial evidence that mPFC both responds to eye contact and uses this to control mimicry behavior. This places mPFC at the core of online social interaction, with a critical role in the subtle decision of who and when to imitate. The results further hint that dysfunction of these social evaluation processes in mPFC would have a detrimental impact on imitation behaviour, as seen in autistic spectrum disorder (Southgate and Hamilton, 2008).

4.6 Conclusion

To conclude, the results of this study reveal different brain systems underlying the inhibition of mimicry and the eye contact effect. More

importantly, we revealed the critical role of mPFC in the interaction between mimicry and gaze. This region acts as a key controller of mimicry by eye contact and performs this function by modulating sensory inputs to action systems. These findings confirm the controlling role of mPFC in social interaction and demonstrate how different components of the social brain, both the mPFC and the MNS, work together to rapidly control spontaneous mimicry according to the social context.

Chapter 5. Mimicry is strategic: likeability and social status interact in driving mimicry

5.1 Abstract

In the workplace, people may respond differently to a nasty boss than to a nasty subordinate. Mimicry is one social response which facilitates affiliation and social interaction. Past studies found that positive features of a target such as niceness, attractiveness and high social status induce more mimicry to the target, while negative features such as low social status and outgroup membership reduce mimicry. The current chapter investigated the joint effect of two critical features, likeability and social status, on mimicry and asked if mimicry is simply driven by the summation of the two features or is more strategically driven by affiliative consequences. Participants were introduced to four actresses in video clips, a nice actress with high status, a nice actress with low status, a nasty actress with high status and a nasty actress with low status. They played a finger tapping game with each actress which measured mimicry. The results revealed a significant interaction between likeability and social status which supports the strategic model of mimicry: participants mimic the nasty actress with high status the most and the nasty actress with low status the least. These findings have important implications for understanding the causes and functions of mimicry in the real world.

5.2 Introduction

Mimicry is the tendency to unconsciously copy the postures, gestures, and mannerisms of others (Chartrand and van Baaren, 2009). Uncovering causes and consequences of mimicry is important for understanding human social behaviour. Past studies on the consequences of mimicry have found that mimicry enhances liking, affiliation and rapport among people (Chartrand and van Baaren, 2009) and promotes one's prosocial orientation to others (van Baaren et al., 2004). Mimicry also leads to a convergence in attitudes and opinions (Chartrand and van Baaren, 2009). Thus, mimicry has been described as a 'social glue' to bind people together (Lakin and Chartrand, 2003).

However, the causes of mimicry are still not entirely clear. Why do people spontaneously mimic each other? And why do they show more mimicry to some people but less to others? Multiple studies reveal that human mimicry behaviour can be enhanced by positive social cues. Participants show stronger mimicry when interacting with an important or likeable target, such as friends, in-group members, high status targets, physically attractive individuals and those with likeable traits (Yabar et al., 2006; Stel et al., 2010b; Bourgeois and Hess, 2008; Cheng and Chartrand, 2003; van Leeuwen et al., 2009). In contrast, mimicry is attenuated by negative social cues. People seldom mimic targets with nasty traits or with visible signs of social stigma (Johnston, 2002). Negative stereotypes on the targets, such as a racist's point of view, can also inhibit mimicry (van Baaren et al., 2003b, 2006; Stel et al., 2010b). These results could all be accounted for under a simple summation model, in which

the amount of mimicry is determined by a simple, stimulus-driven mechanism which sums up the positive and negative features of the target and mimics more when more positive features are present.

In contrast to this summation model, it has been hypothesised that mimicry is caused by a more sophisticated and strategic mechanism (Lakin and Chartrand, 2003; Lakin et al., 2003, 2008). As mentioned above, a major consequence of mimicry is to enhance liking and affiliation toward the mimicker (Chartrand and Bargh, 1999; Maddux et al, 2008; Bailenson and Yee, 2005; Ashton-James et al., 2007). A strategic mimicry mechanism could take advantage of this outcome to make people unconsciously mimic more when a social advantage will result. Under this model, mimicry is not just a summed response to social cues, but is strategically driven by an estimation of the consequences of the mimicry. Where there is a stronger strategic need to affiliate perhaps because a target has high social status, a participant would show more mimicry.

This strategic hypothesis of mimicry was supported by some studies where people who have a goal to affiliate with others show more mimicry behaviours (Lakin and Chartrand, 2003). Some other evidence can be seen in studies where being ostracized by others or surrounded by a disharmonious social atmosphere can increase mimicry (Over and Carpenter, 2009a; Lakin and Chartrand, 2003). However, few experiments have directly distinguished between a feature summation model of mimicry and a strategic model of mimicry.

In the present chapter, we aim to test these two models of mimicry. Previous studies on the causes of mimicry have only investigated one social

factor at a time, which makes it difficult to distinguish these two models. Here, we directly compare two social factors, likeability and social status, and explore their joint effect on mimicry. Undergraduate subjects were introduced four actresses, apparently for a memory task. Likeability and social status of each actress were manipulated via vignettes which characterized the actresses as nice with high status, nice with low status, nasty with high status and nasty with low status. After memorizing the vignettes, participants performed a simple finger tapping task (Brass et al., 2000, 2005; see 1.2.1) which provides a measure of mimicry to each of the four actresses. Previous studies suggest that when social status is equal or unknown, people mimic nice targets more than nasty ones (Stel et al., 2010b), and when personality is unknown, people mimic high status targets more than low status ones (Mastrop et al. 2011; Cheng and Chartrand, 2003; Giles and Powesland, 1975; Brody and Stoneman, 1981; Kwaadsteniet and van Dijk, 2010).

The two different models of mimicry provide different predictions for the combination of these two factors. If mimicry is driven by a simple summation of positive or negative features of the stimuli, the results should show a linear response to a combination of likeability and status, with the highest mimicry for the nice, high status actress. In contrast, if mimicry is strategically driven by the needs to affiliate with others, then the mimicry for the nice, high status actress should not be the highest because it is not necessary to strategically use mimicry to build an affiliation with a target who is already nice. Instead, participants will mimic the nasty actress with high status more than other actresses, as this actress is potentially influential but also presents the greatest challenge in building affiliation, so participants have to recruit more

mimicry to get along well with them. The present study will test these alternatives.

5.3 Materials and Methods

Participants

Twenty-four undergraduates from the University of Nottingham gave their informed consent to participate in this study (19 females, 5 males; mean age 20.1; age range 18 -21; S.D. 1.23 years), and were paid for their participation. All were right-handed, native English speaker and naïve as to the purpose of the study.

Actress memory stimuli

Videos of four different actresses (two aged 16 years, two age 25 years) were used. In preparing the videos, eighteen women at age 16 and seventeen women at age 25 were filmed, and the clips were all rated for attractiveness and likeability by twenty-four pilot undergraduates (who did not take part in the main experiment). The four videos with the most similar ratings on both scales were chosen for the study, to ensure that actress characteristics were accurately matched.

A booklet of four pages was prepared, each with a profile photo and a vignette that described a fictitious person. In the vignette (see 5.7 Appendix), participants were informed of the actress' age (16 or 25) and current education stage (school or postgraduate), which was manipulated to arouse either a low or a high social status for the character. Age and education were used as proxies for social status because previous studies show that older / more educated students are regarded as higher social status than younger /

less educated student (Hollingshead, 1957, 1975; Benoit-Smullyan, 1944; Feldman and Dodge, 1987). The vignette also mentioned good or bad behaviour that the actress did in the past, which was designed to invoke either a nice or a nasty personality for the character. These vignettes created four different actresses: a nice one with high status, a nice one with low status, a nasty one with high status, a nasty one with low status. The structure and the tone of the vignettes were similar to Kozak et al., (2006).

Finger tapping task

Different from studies in previous chapters, here we used another SRC paradigm to measure mimicry—the 'finger tapping task' (Brass et al., 2000; 2005; Bertenthal et al., 2006; see 1.2.1). In each trial, participants first watch a three-second video (Figure 5-1). At the onset of the video, an actress appears with her left hand placed below her chin and her face looking away from the camera. A white square was superimposed between her index and middle finger. Then the actress naturally moved her head towards the camera which resulted in a direct gaze and a little smile, like an everyday greeting. This gaze cue was designed to maximise the potential for mimicry, because previous chapters show that direct gaze enhances the tendency to mimic. After the gaze stimulus, a number (1 or 2) appeared on the white box and her left hand performed a finger tapping movement either using index finger or middle finger. The participants task was to respond to the number stimulus (1: index finger, 2: middle finger) as fast as possible and ignore the actress' hand movement.
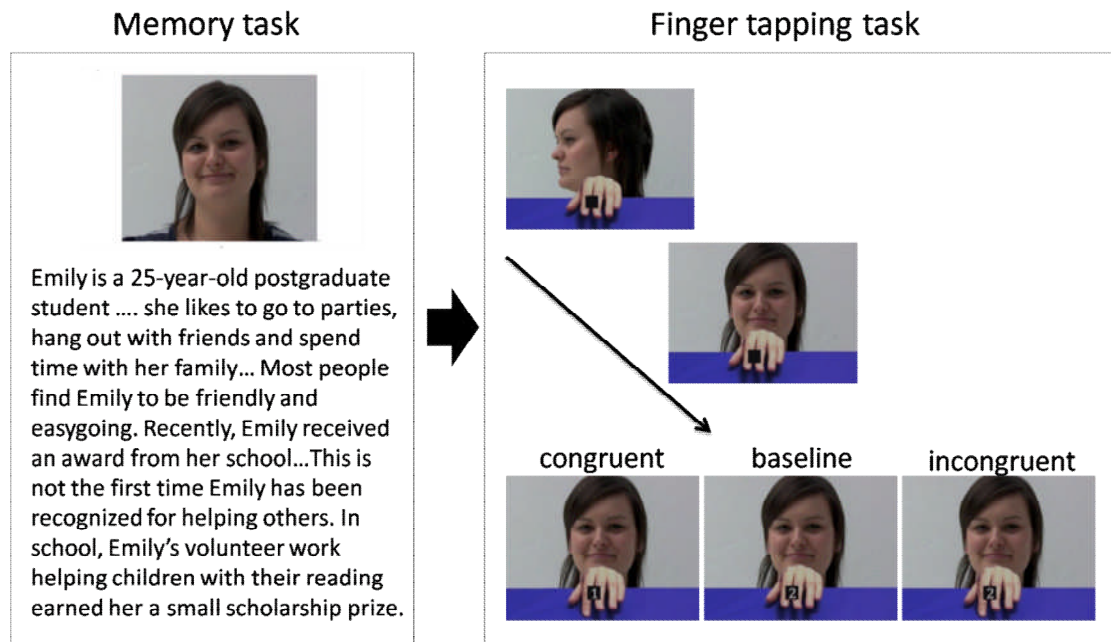
Figure 5-1. Examples of the procedure and stimuli. Participants had to complete one page of memory task and one block of finger tapping task each time (see text for details).

In congruent trials, the actress' hand executed an identical finger movement to the instructed movement, while in incongruent trials the movement executed by her hand on the screen was different from the instructed movement. In baseline trials, her hand on the screen did not perform any hand movement, only the number appeared (Brass et al.,2000, 2005). Past studies found that observing an action automatically activates the motor representation of that action and participants unconsciously and spontaneously mimic the moving finger in the finger tapping task (Brass et al., 2000, 2005; Bertenthal et al., 2006). Therefore in congruent trials they were facilitated by the mimicry of observed action while in incongruent trials participants had to enforce the intended action against the mimicry of observed action; their actions were not influenced in the baseline trials. As in previous chapters, mimicry can be assessed by calculating the congruency

effect (CE)—the reaction time difference between congruent trials and incongruent trials.

In order to make participants familiar with the finger tapping task, they performed a practice session before all the testing sessions. There were 5 incongruent trials, 5 congruent trials and 5 baselines presented randomly in the practice session. Then the task in testing sessions involved 16 incongruent trials, 16 congruent trials and 8 baselines in a randomized order. Delay between the end of head movement and the onset of number was either 200 or 800 ms, to make participants unable to predict the onset of the number. Matlab software and Cogent was used for stimulus presentation and data collection.

Procedure

Each participant was tested individually. First, participants were asked to memorize one page of vignette about one of the four actresses. Then they performed the finger tapping task with that actress featured in the video stimuli. This procedure was repeated for the other three actresses (Figure 5-1). Order of actress presentation was counterbalanced across participants, as was the pairing of each actress' face with each vignette. At the end of the experiment, each participant was required to complete a memory questionnaire about each actress' age, likeability and social status, as a manipulation check. Participants did multiple choices on the actress' age and name, and rated each actress' likeability and physical attractiveness on a five point scales, ranging from 1 (not very likeable/attractive) to 5 (very likeable/ attractive).

5.4 Results

Finger tapping task

To remove trials in which participants did not attend to the number stimuli, incorrect responses (0.05%) were excluded from the analysis, as were all RTs smaller than 100ms or greater 800ms (0.13%). To minimize the effect of outliers, we also excluded RTs that were greater than two standard deviations from the conditional means of each participant (0.18%). The congruency effect (CE) for each participant was calculated by subtracting reaction time (RT) in congruent trials from RT in incongruent trials.

A two-way repeated measures analysis of variance (ANOVA) was conducted on participants' CE with actress' likeability (nice, nasty) and social status (high, low) as variables. The two-way analysis revealed a significant interaction on CE: likeability $\times$ social status ($F_{(1,23)}$=4.70, p<0.041) (Figure 5-2a). The CE to the nasty actress with high status was the largest (M=24.82ms), followed by the nice actress with low status (M=18.04ms) and nice actress with high status (M=17.26ms); the nasty actress with low status induced the smallest CE (M=6.92ms). Post hoc t-test showed the CE to nasty actress with high status is significantly different from the CE to nasty actress with low status (t $_{(23)}$ = 3.42, p<0.016) (Figure 5-2a). There was no main effects of likeability (p=0.594) or social status (p=0.142) on CE.
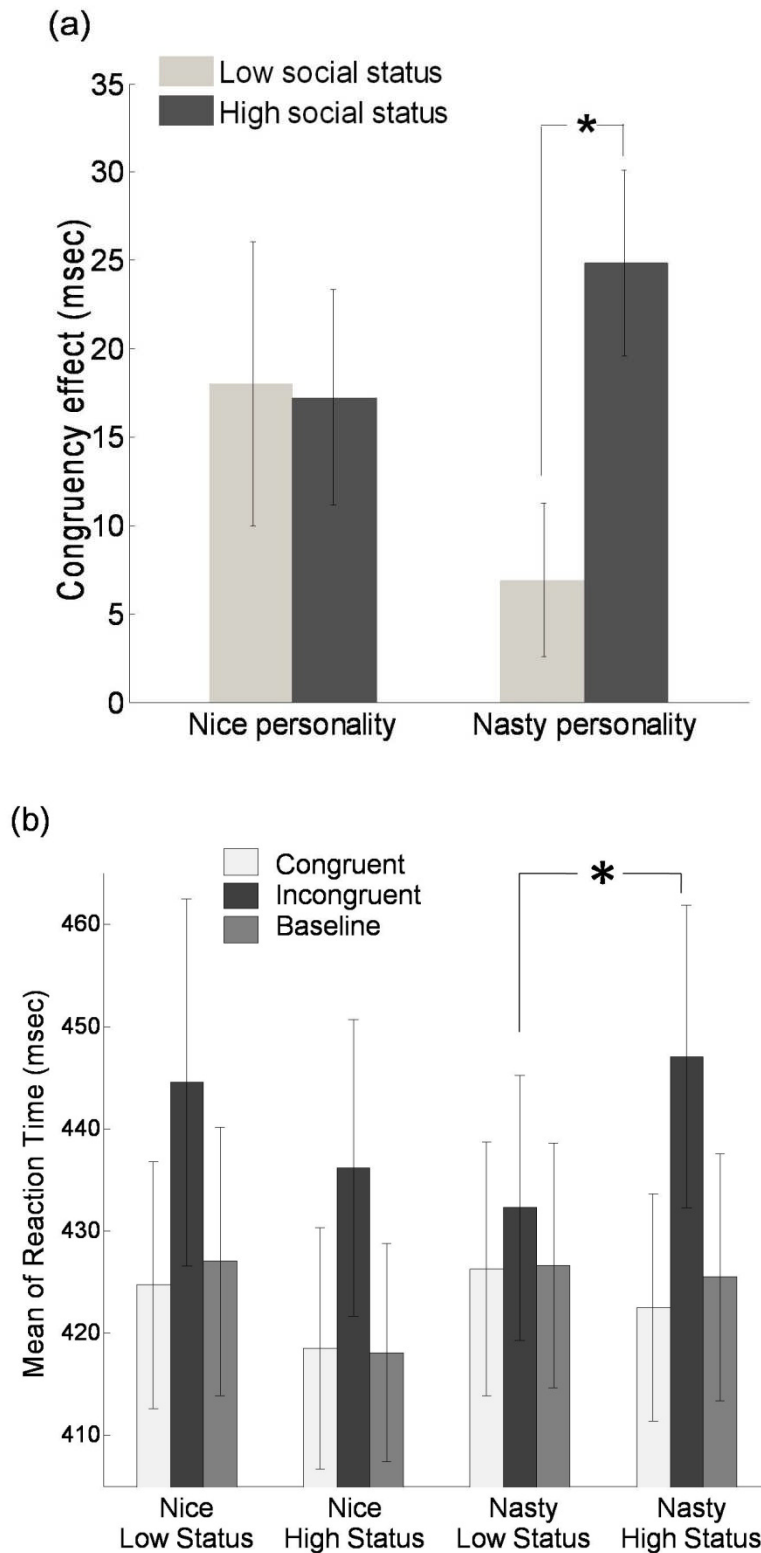
Figure 5-2. Mean congruency effect (a) and Mean reaction time on congruent, incongruent and baseline trials (b) for each of the four actresses. Asterisk represents the statistically significant difference between two bars. Vertical bars indicate S.E

In order to further explore the underlying mechanism of this two-way

interaction, we performed a three-way ANOVA on participants' mean RT with congruency (congruent, incongruent, baseline), actress' likeability (nice, nasty) and social status (high, low) as variables. First, the three-way ANOVA analysis revealed a significant main effect of congruency ($F_{(1,23)}=13.6$, $p<0.001$); on average, responses were slower for incongruent trials (M=440ms) than for baseline trials (M=426ms) and congruent trials (M=423ms). Other main effects such as likeability (p=0.770) or social status (p=0.773) were not significant. Second, there was a significant interaction on RT: Congruency × Likeability × Social status ($F_{(1,23)}=4.70$, $p<0.041$) (Figure 5-2b), which was consistent with the two-way ANOVA results. Post hoc t-test revealed that the significant CE difference between nasty actress with high status and nasty actress with low status (Figure 5-2a) was due to the significant RT difference in their incongruent trials ($t_{(23)} = 2.25$, $p<0.034$), as the congruent and baseline responses in the two groups were statistically unaltered (Figure 5-2b). Other interactions such as Congruency × Likeability (p=0.594) or Congruency × Social status (p=0.142) were not significant on mean RT.

Manipulation check

Participants answered all age-related questions correctly (0% error rate) in the memory questionnaire, which indicated the success of social status manipulation. The scores on likeability and attractiveness in the questionnaire were all further analysed with a two-way repeated measures ANOVA (with personality priming and social status priming as two variables). It revealed a significant main effect of personality priming on likeability rating ($F_{(1,11)}=24.62$, $p<0.001$), as well as on attractiveness rating ($F_{(1,11)}=18.96$, $p<0.001$); each actress' likeability and attractiveness, which were rated as equal before any

personality priming, were rated higher when they were primed with a nice personality and were rated lower when they were primed with a nasty personality (Figure 5-3a). A Pearson's correlation test also revealed a significant positive correlation between likeability rating and attractiveness rating (F=54.38, p<0.001). There was no main effect of social status priming on either the likeability score (p=0.924) or attractiveness score (p=0.972).

We also examined the relationship between the likeability/attractiveness scores and the corresponding CE to that actress. As the scores of likeability and attractiveness were positively correlated, we used their sum (ranges from 2 to 10; 10 is most likeable and attractive) as the independent variable in the linear regression test to see how it predicts the CE. Dummy variables were included as the controlling of repeated measures on the same participant. The results revealed no significant linear models for the prediction of CE by the sum score within each type of the actress; however, when actresses with the same status (high or low) were analyzed together (Figure 5-3b), we found a significant linear model in the low status group suggesting a positive correlation between the sum score and CE (R^2=0.728, p=0.014) and a marginally significant linear model in high status group suggesting a negative correlation between the sum score and CE (R^2=0.656, p=0.077). These two linear models suggest that the more participants like the low status actress or feel her attractive, the stronger the CE was; inversely, the more participants dislike the high status actress or feel her not attractive, the stronger the CE was induced.
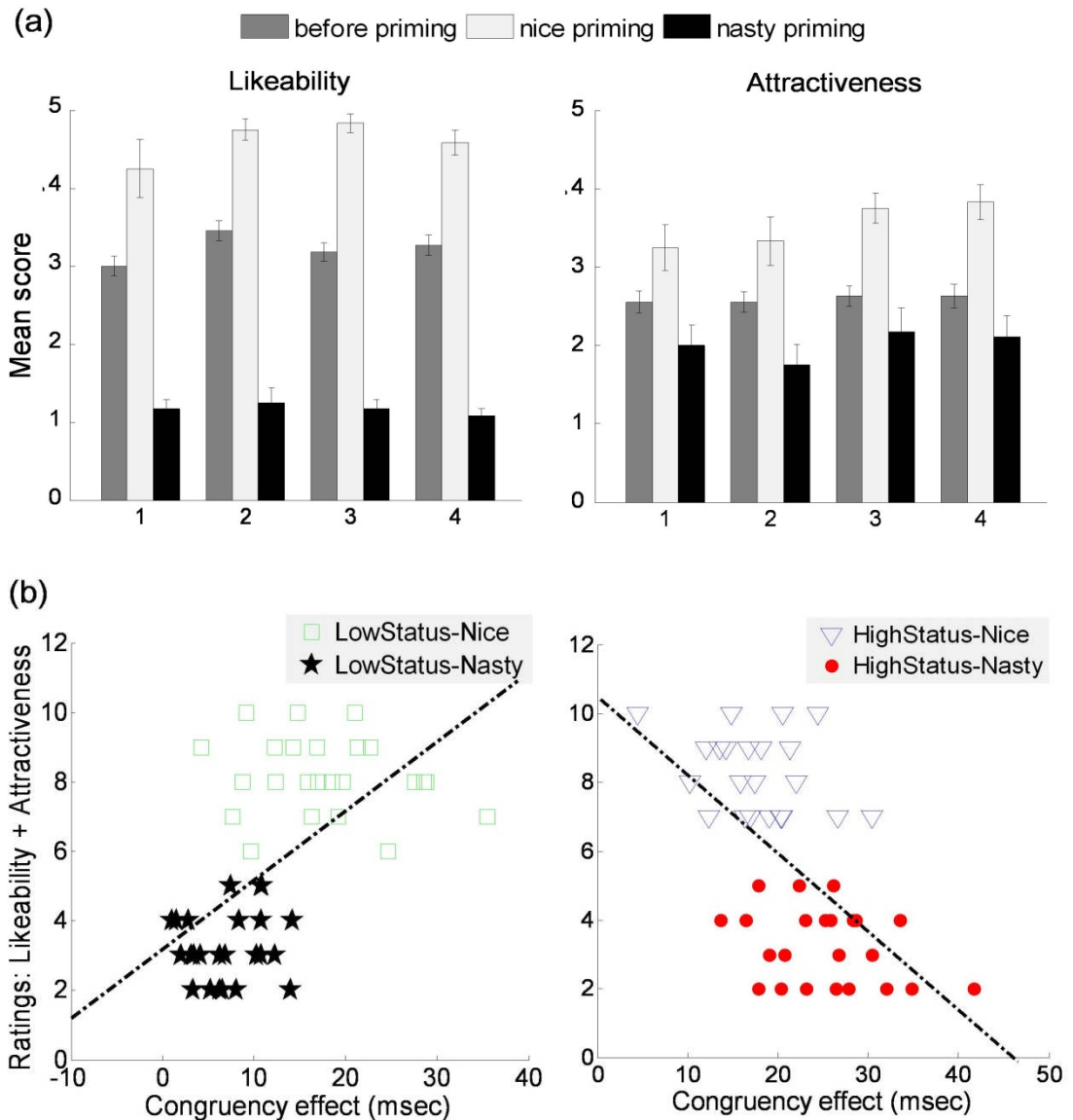
Figure 5-3. Mean scores of likeability and attractiveness for each actress in different priming conditions (a) and the linear regression test for the relationship between the sum score (likeability + attractiveness) and CE induced either by low status actresses or high status actresses (b). Along the horizontal coordinate in (a), 1 and 2 represents two actresses aged 28 and 3 and 4 represents another two actresses aged 16. "Before priming" represents the scores in the pilot study where there was no priming manipulation. Vertical bars indicate S.E. The black dot line in (b) represents the curve estimation of the two linear models.

5.5 Discussion

The results of current study demonstrated that likeability and social status interact in modulating mimicry. Specifically, likeability enhanced mimicry when the actresses were low status but inhibited mimicry when the actresses were high status. The results also support the second theoretical prediction that mimicry is strategically driven by consequence, as participants mimic the nasty actress with high status most.

Implications for social psychology

Our study aimed to distinguish two models of mimicry, a simple summation model and a strategic model. We found that mimicry is not simply driven by the summation of the positive features of the actress; instead, it is strategically driven by the consequences of mimicry. Negative features, such as a nasty personality, usually inhibit people's mimicry to the target (Stel et al., 2010b; Johnston, 2002), so did the nasty actress with low status in current study (Figure 5-3b, left). However, this inhibitory effect by a negative feature is completely reversed when the nasty actress had a higher social status. At that point, although the actress is nasty, as long as she is high status and dominant to participants, they have to strategically use mimicry as an effective and efficient way to get along with this important but nasty actress. In contrast, intermediate levels of mimicry were seen for the two nice actresses, regardless of status.

This conclusion on the strategic nature of mimicry is consistent with a recent study about the effect of the romantic relationship on mimicry. People usually mimic an attractive target more than an ordinary appearance target

(van Leeuwen et al., 2009), however, Karremans and Verwijmeren (2008) found that participants who were in a relationship mimicked an attractive opposite-sex target much less than those not involved. The romantic relationship suppressed the facilitative effect of an attractive opposite-sex target on mimicry, which they explained is a strategic way to shield current relationship. Similarly, it has also been reported that people strategically mimic facial expressions to maintain and regulate social relationships. Bourgeois and Hess (2008) found that people mimic positive expressions displayed by a target such as happiness, but never mimic negative expressions such as anger; more importantly, they only mimic sadness when the target is close to them (a friend or in-group member). These studies are consistent with our conclusion that, despite being an unconscious, rapid and spontaneous phenomenon, mimicry is not determined by a simple stimulus-driven summation mechanism, but is deployed strategically with consideration of the consequences of the mimicry act.

It is important to note that the actions (finger tapping) we used here to measure mimicry were not indicative of social status. Recent research demonstrated that people mimic status-related behaviours (such as body expansion as a dominance behaviour and body constricted as a submissive behaviour) differently from status-unrelated behaviours (Mastop et al. 2011). As mimicking high-status target's dominant behaviours may destroy hierarchical balance (Strong et al., 1988), people only mimic the submissive behaviours but seldom mimic the dominant behaviours; instead they complement the dominant behaviours. In the future it will be interesting to see how likeability and social status interact on mimicry when targets are doing

status-related behaviours and whether it is still strategic-driven.

One possible criticism of our approach is the use of a simple rapid finger tapping task rather than the more naturalistic paradigms commonly used to study the 'chameleon effect' (Chartrand and van Baaren 2009). Though our SRC paradigm puts participants in a more controlled and minimal context compared to the natural interaction paradigm (see 1.1.1), participants in both paradigms are unaware that the experimenter is recording mimicry behaviours or that mimicry is the subject of the investigation. Thus, both paradigms investigate unconscious, spontaneous mimicry. Moreover, consistent results have been obtained using both approaches (Leighton et al., 2010; Lakin and Chartrand, 2003). Thus the congruency effect measured by controlled paradigm can be regarded as equivalent to the unconscious mimicry measured by naturalistic studies (Heyes, 2011).

There are advantages to our paradigm, because it allows us to investigate more factors in a single study, which was critical for this experimental design. Our video stimuli and finger tapping task provide careful control of critical features like stimulus-response timing, and of factors which might modulate mimicry, such as eye contact (Chapter 2 and Chapter 3) and emotion (van Barren et al., 2006). Finally, the controlled paradigm allows us to determine the underlying mechanism of the modulation. Naturalistic paradigms only measure the increased/decreased number of mimicry behaviours caused by a certain modulator, but without providing information on how the modulator increases/decreases mimicry. Here the paradigm can inform us about the cognitive processes underlying control of mimicry.

Neurocognitive theories of mimicry

To understand the mechanism underlying the interaction, we examined the exact RT in congruent, incongruent and baseline trials within two nasty groups (Figure 5-2b). We found that in incongruent trials, the RT to nasty actresses with high status was much slower than to nasty actresses with low status; but in congruent and baseline trials, they were same. As the time difference between incongruent and baseline trials reflects the process of inhibition of mimicry, this substantial slower RT in incongruent trials suggests that participants need more time and efforts to inhibit the mimicry to a nasty target with high status than to a nasty target with low status. Thus, it is the modulation of the inhibition of mimicry by the social status of the nasty actress that contributes to this interaction. Slower RT on incongruent trials here contrasts with another study where direct gaze modulates mimicry by enhancing the RT of congruent trials (Chapter 2 and Chapter 3), and suggests that different cognitive modulation mechanisms may be at work.

Our findings also have important implications for understanding the neurocognitive causes and control of mimicry. Research in cognitive neuroscience suggests that the mirror neuron system provides the mechanism of mimicry (Iacoboni et al., 1999), but recent theories emphasize how these systems can be modulated and controlled by other components of the social brain (Southgate and Hamilton 2009, Teufel et al., 2010). Our results support this idea, demonstrating sophisticated and strategic control mechanisms which make mimicry more adaptive and efficient in social interaction. Such mechanisms might well rely on brain regions beyond the mirror neuron system. As patients with autism, echolalia and echopraxia often

display improper and non-adaptive mimicry (Hamilton, 2008), it is plausible that they suffer from the dysfunction of this strategic control of mimicry and cannot benefit from the affiliative consequence of mimicry. Future research is needed to validate this explanation.

5.6 Conclusions

In conclusion, the current research has demonstrated that mimicry is not just an automatic, simple stimuli-driven response; instead, it is a sophisticated response strategically driven by affiliative consequences. Social status and likeability interact in driving mimicry, which makes mimicry more adaptive and efficient in social interaction. These findings help us understand the causes and functions of mimicry and learn more about human non-verbal social behaviour.

5.7 Appendix

Table 5-1. Vignettes for each type of actresses

Nice with High Status	Emily is a 25-year-old postgraduate student at Cambridge University. She works very hard in the lab and will finish her PhD in biology next year. Out of the lab, she enjoys working in the Student Union. At the weekend, Emily likes to go to parties, hang out with friends and spend time with her family who live nearby. Most people find Emily to be friendly and easy-going. Recently, Emily received an award from her school. She tutored several undergraduates in a biology class and helped them improve their grades. The professor learned that Emily was helping them without asking for any pay in return and told the university. Emily received a service award from the university. This is not the first time Emily has been recognized for helping others. In school, Emily's volunteer work helping children with their reading earned her a small scholarship prize.
Nasty with High Status	Emma is a 25-year-old PhD student at Oxford University. She majors in Chemistry, and is also interested in political science. Outside class, she doesn't participate in any intramural activities, because she considers them to be boring and a waste of time. At the weekend, Emma prefers to spend time alone instead of with friends or with her family. Most people find Emma to be arrogant and unapproachable. Recently, Emma was in severe trouble at her work. She copied a friend's lab report and submitted it as her own. The professor found out and reported it to the university. Emma is now on academic probation. This is not the first time Emma has been caught cheating. In secondary school, she plagiarized on a term paper and was suspended for three days.

Nice with Low Status	Kate is a 16-year-old girl. She just finished her GCSEs and is starting her A-levels. In extracurricular activities, she plays football for her school team and gets on well with other players. In her daily life, she is respectful and kind to everyone whom she meets. She remembers every friend's birthday, and is always keen to organize a wonderful party for them. One thing that is quite unique about Emily is her passion for helping animals. She devotes a great deal of time helping to raise money for local animal shelters as well as volunteering one day a week working at the local humane society. After her A-level, Emily hopes to either pursue a degree in veterinary medicine or public health.
Nasty with Low Status	Rachel is a 16-year-old girl. She is starting her A-level in chemistry. Although she is intelligent at school and has always had good marks for coursework, most classmates think she is arrogant and unfriendly. She often teases her classmates when they get bad marks, while boasting about her own success. Outside class, she spends time alone reading novels, never going to parties with her classmates. She once said her classmates were stupid and their parties are just waste of time and money. She is known for her arrogance and thinks she is the most attractive girl in the school. Because of this, she doesn't have many close friends. Rachel has been telling everyone that she will go to Oxford in the future. However, her teachers are not sure if she will get in.

Chapter 6. Prosocial priming of mimicry depends on who is prosocial

6.1 Abstract

People have a tendency to unconsciously mimic others. This mimicry is flexible and can be modulated by multiple social factors. Past research in social psychology revealed a close relationship between prosociality and mimicry, with more prosocial priming leading to more mimicry. However, some recent studies show that priming antisocial information such as ostracism can also enhance mimicry. The present study aims to clarify the relationship between pro/antisocial priming and mimicry, and to test if the self-relatedness of the priming stimuli alters how mimicry is primed. Participants were primed by pro/antisocial behaviors either from a first-person or third-person perspective. Experiment 1 demonstrates that priming antisocial behavior by a third party leads to increased mimicry. Experiment 2 replicated this effect, but also demonstrates that priming prosocial behavior by the self leads to increased mimicry. These findings of contrasting priming effects for first-person and third-person pro/antisocial primes demonstrate the subtle modulation of mimicry by social primes and hit at the underlying mechanisms.

6.2 Introduction

People have a tendency to unconscious imitate other's actions, termed "mimicry" (Chartrand and Bargh, 1999). This mimicry plays a critical role in creating social bonds between people (Chartrand and van Baaren, 2009) and

making social interaction smoother (Chartrand and Bargh, 1999). Social psychology suggests that mimicry is flexible and context-sensitive, and can be modulated by multiple social factors such as motivation, attractiveness, friendship and social status (Chartrand and van Baaren, 2009).

Recent research revealed a close relationship between mimicry and prosociality, with bidirectional causality (Chartrand and van Baaren, 2009). Mimicry causes people to become more prosocial in general, not just toward the person whom they are mimicking or who is mimicking them, but to others as well (van Baaren et al., 2004; Chartrand and van Baaren, 2009). For example, people after a mimicry interaction sit closer to others (Ashton-James et al., 2007), increase helpfulness toward strangers (van Baaren et al., 2004; Fischer-Lokou et al., 2011), donate more money to a charity (Stel et al., 2008a) and share a converging attitude with others (Maddux et al., 2008). Similarly, prosociality leads to more mimicry. Early work demonstrated that posture sharing was observed in classroom situations in which rapport already existed (Bernieri, 1988; LaFrance, 1979, 1982). People with a prosocial self-construal or high empathy ability tend to mimic others more than ones with an antisocial self-construal or low empathy ability (van Barren et al., 2003b; Chartrand and Bargh, 1999). Simply priming people with a prosocial goal or attitude increases their mimicry behavior (Lakin and Chartrand, 2003; Leighton et al., 2010). Even merely exposing people to prosocial stimuli such as prosocial words or sentences is sufficient to enhance mimicry (Lakin and Chartrand, 2003; Leighton et al., 2010; Cook and Bird, 2011a).

In contrast, three studies recently found that in some situations, antisocial primes can also enhance mimicry. People who experienced social ostracism

(Lakin et al., 2008) or felt extremely distinct from the majority (Uldall et al., 2011) mimic a subsequent interaction partner more than people in a control condition. Over and Carpenter (2009a) showed that just witnessing someone being excluded (a third-party ostracism priming) significantly enhances mimicry in children. They explained that social ostracism induces a motivation to affiliate with others and children strategically used mimicry to ingratiate themselves with other group members. This explanation is compatible with a battery of studies showing that witnessing social conflict activates one's prosocial motivations such as empathy/sympathy, consolation and helping behavior towards the victim (Fujisawa et al., 2005, 2006; Vaish et al., 2009; Vitaglione and Barnett, 2003). However, enhancement of mimicry by antisocial behaviors priming seems to contradict the larger body of literature linking mimicry to prosocial primes. It is not clear why these antisocial primes per se failed to prime people with an antisocial goal or attitude (e.g. exclude others) (Twenge et al., 2007; Over and Carpenter, 2009b) and thus decrease mimicry as previous studies showed (Leighton et al., 2010; Chartrand and van Baaren, 2009). Thus, the literature on the priming of mimicry by pro or antisocial stimuli seems very mixed.

Studies of priming in other automatic stereotypic behavior have also yielded varied results. For example, priming of the concept of 'elderly' caused participants to walk slower (Bargh et al., 1996) and priming of the concept of intelligence caused participants to perform better on a general knowledge questionnaire (Dijksterhuis et al., 1998). However, priming of individual exemplar of elder (e.g. 89 years old Dutch Queen Mother) and intelligence (e.g. Einstein) can lead to the opposite effect (Dijksterhuis et al., 1998), with

quicker walking speed and worse performance on the intelligence questionnaire. Dijksterhuis et al., (2001) suggest these opposing effects can be best understood in terms of how the prime is processed in relation to the self, because the representation of social primes according to the self can lead to either behavioral "assimilation" or "contrast" effect. It is possible that a similar self-relatedness of primes is important in understanding pro/antisocial priming in the context of mimicry. The present study allows us to test this possibility.

Many previous studies of social priming on automatic behaviors measured the impact of the prime on a single, natural setting task (e.g. walking speed or number of mimicry actions) and all manipulations were conducted between participants (e.g. participants were separately assigned to different priming groups). Our approach in present study builds on the recent finding that mimicry responses can be recorded in more carefully controlled SRC tasks with multiple trials per participants (see a review paper by Heyes, 2011) and that these SRC tasks show the same priming effects as natural encounters (Leighton et al., 2010; Cook and Bird, 2011a; Heyes, 2011). We adopted a within-subjects priming design before these SRC tasks and implemented all priming stimuli to each participant, to remove effects due to individual differences in mimicry. Specifically, priming was induced by means of a traditional 'scrambled sentence task' (Srull and Wyer, 1979) and each participant was primed by three types of social behavior (prosocial, antisocial and non-social). After each type of prime, we used a 'finger tapping task' to measure their mimicry (see 1.2.1). In each trial, participants had to move their index or middle finger in response to a number while viewing incongruent or

congruent finger movements on a computer screen. Previous research found faster responses to congruent than incongruent actions and took this congruency effect as an accurate and reliable measure of mimicry (Heyes, 2011). Here in two experiments, we aim to examine whether and how pro/anti social priming influences this congruence effect.

6.3 Experiment 1: Does pro/anti social priming alter mimicry?

The first study aimed to test if priming of pro/anti social behavior has an impact on mimicry in the context of our experimental task. Our design is very similar to Leighton et al. (2010), though this study was conducted before we were aware of Leighton's findings. Participants had to complete scrambled sentences where they were semantically primed by a series of pro/anti/non-social behaviors between two fictional characters. We predicted that if other's prosocial behavior dominates one's own automatic behaviour, we should see stronger mimicry in prosocial conditions as shown by Leighton et al., (2010). However, if priming other's antisocial behavior somehow increases one's prosocial motivation, just as the third-party ostracism priming did (Over and Carpenter, 2009a), we might see more mimicry in antisocial primes.

## 6.3.1 Materials and Methods

Participants

Nineteen students from the University of Nottingham gave their informed consent to participate in this study (14 females and 5 males; average age 23.8; S.D. 2.81 years), and were paid for their participation. All were right-handed,

proficient in the English language, had normal or corrected-to-normal vision and naïve as to the purpose of the study.

Stimuli

The priming manipulation took the form of "Scrambled Sentence Test" (Srull and Wyer, 1979; see 1.1.1) in an A4 booklet. For each test sentence, two words were already presented in a correct order in the answer sheet and participants were required to use other six words out of a seven words list, to construct a grammatically and semantically correct eight-word sentence. Three types of scrambled-sentences were constructed (Figure 6-1): one was designed to prime a prosocial behavior between two fictional characters (e.g., 'John gives Laura a warm and affectionate hug', 'Frank and Mary cooperate to make model planes'); another was to prime participants with an antisocial behavior between two characters (e.g., 'Sam makes Jane weep for a long time', 'Paul destroys Angelina's new toy train on purpose'), and a third was intended to prime neutral non-social information (e.g., 'A rainbow is made of seven different colours', 'London is the capital of the United Kingdom').

We adopted the 'finger tapping task' to measure mimicry (Brass et al., 2000, 2005; Bertenthal et al., 2006). In the task, two-frame video sequences of a hand were displayed on a computer monitor (Figure 6-1). The first frame displayed a white blank box in the middle and around it a left hand was naturally stretched on a plane. The second frame displayed two numbers (1 or 2) on the middle white box and meanwhile the left hand was performing an finger tapping movement either using index finger or middle finger. The interval between two frames varied (600, 1200, 1800ms).
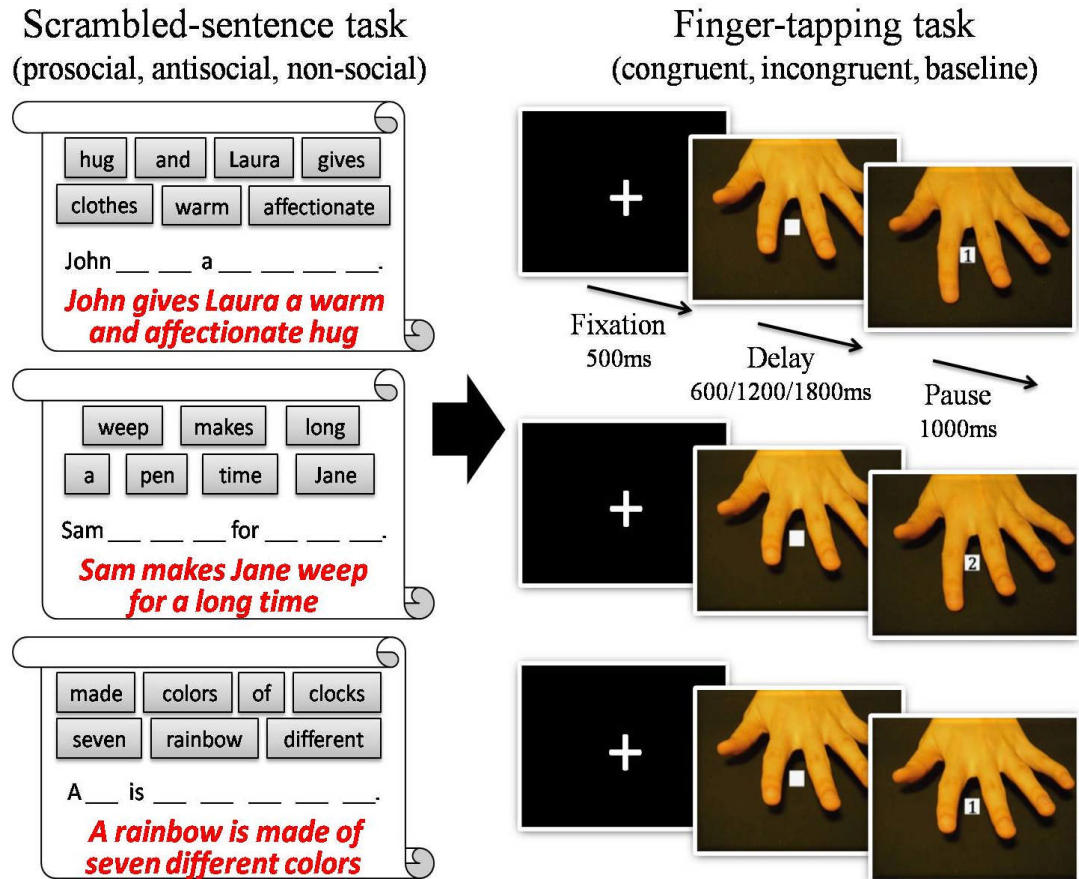
Figure 6-1. Examples of the priming sentences in the scrambled-sentence task and the hand movement stimuli in the finger-taping task. Each time participants had to complete one page of scrambled sentences describing pro/anti/non social behaviours on a booklet and then one block of finger tapping task on a computer where they had to respond to a number cue in the middle of the screen and ignored a congruent/ incongruent/still hand movement stimuli on the background. They had to complete twelve pages of scrambled-sentence task and twelve blocks of finger tapping task alternately.

Design and procedure

Participants were told that they were taking part in two independent tests of language proficiency and motor control ability, and that the two tests would be alternated to reduce boredom (Bengtsson et al., 2011). They had to complete twelve pages of scrambled-sentence task and twelve blocks of

finger tapping task. Each page of scrambled sentence task contained four sentences and they were all designed to prime the same type of social behaviors (prosocial, antisocial or non-social). Participants could use pencil to write anything on the page for assistance but had to complete the four sentences as quickly as possible. In order to consolidate the priming effect, participants were also required to read their answers to the experimenter for a correction check when they finished each page. The page sequence for testing was randomized and different for each participant, to make sure that they were primed by a specific social behavior in a different sequence.

Every time participants finished one page of scrambled sentence task, they proceeded to a block of finger tapping task. Here, the finger tapping task was identical to the one we used in Chapter 5. In each trial, participants were instructed to move their index or middle finger in response to a number (1: index finger, 2: middle finger) appeared in the white box while viewing incongruent or congruent finger movements around the white box. In congruent trials, the hand in the video frame executed an identical finger movement to the instructed movement, while in congruent trials the movement executed by the hand on the screen was different from the instructed movement. In baseline trials, the hand on the screen did not perform any hand movement, left only the number appearing. Participants were asked to respond to the number as quickly as possible and to disregard the moving finger in the background. Past studies found that observing an action automatically activates the motor representation of that action and participants unconsciously and immediately mimic the moving finger in the finger tapping task (Brass et al., 2000, 2005; Bertenthal et al., 2006). Therefore in congruent

trials they were facilitated by the mimicry of observed action while in incongruent trials participants had to enforce the intended action against the mimicry of observed action; their actions were not influenced in the baseline trials. Mimicry is assessed by calculating the congruency effect (CE)—the reaction time difference between congruent trials and incongruent trials. There were 12 incongruent trials, 12 congruent trials and 12 baselines in a block of the finger tapping task and they were in a pseudo-randomized order.

In order to make participants familiar with these two tasks, they performed a practice session before all the testing sessions. There were three scrambled sentences for practice, each exemplifying one type of priming (prosocial, antisocial and non-social). A short version of the finger tapping task was also prepared for practice, with 5 incongruent trials, 5 congruent trials and 5 baselines trials in a pseudo-randomized order. Matlab software was used for all hand stimulus presentation and data collection.

6.3.2 Results and Discussion

To remove trials where participants did not attend to the number stimuli, incorrect responses (0.04%) were excluded from the analysis, as were all reaction times (RT) smaller than 100ms or greater 800ms (0.06%). To minimize the effect of outliers, we also excluded RTs that were greater than two standard deviations from the conditional means of each participant (0.12%). The CE for each participant was calculated by subtracting RT in congruent trials from RT in incongruent trials. Figure 6-2 shows both CE and RT data for each priming group.

In order to test whether mimicry was influenced by the priming sentences

in our experimental task, a repeated measures analysis of variance (ANOVA) was conducted on mean RT with congruency (congruent, incongruent, baseline) and primes (prosocial, antisocial, non-social) as variables. The analysis revealed a significant main effect of congruency ($F_{(2,36)}=26.3$, $p<0.001$) with a faster response in congruent trials ($M=429$ms) and a slower response in incongruent trials ($M=447$ms); the response in baseline trials was intermediate ($M=436$ms). This main effect of congruency confirmed the success of mimicry measurement in our experimental task. In addition, the ANOVA also revealed a significant interaction between congruency and primes ($F_{(4,72)}=3.52$, $p<0.011$), which suggests that mimicry was modulated by the priming sentences.

To further look into the priming effect on mimicry, a repeated measures ANOVA was conducted on mean CE with primes (prosocial, antisocial, non-social) as variables. The analysis revealed a significant main effect of primes on CE ($F_{(2,36)}=4.76$, $p<0.015$) (Figure 6-2a), which is consistent with previous congruency × primes interaction on RT. Specifically, the antisocial priming group induced a stronger CE ($M=25.7$ms) than the non-social ($M=14.8$ms) and prosocial priming group ($M=13.6$ms). Post hoc t-test showed the CE in antisocial priming group is significantly larger than the one in non-social ($t_{(18)} = 2.52$, $p<0.022$) and in prosocial priming group ($t_{(18)} = 2.81$, $p<0.012$), but there was no difference between the prosocial and non-social priming groups ($t_{(18)} = 0.24$, $p=0.813$).

These results suggest that priming pro/antisocial behaviors between two fictional characters does have an impact on mimicry in the context of our experimental task. In particular, priming antisocial behaviors enhances

mimicry while priming prosocial does not.
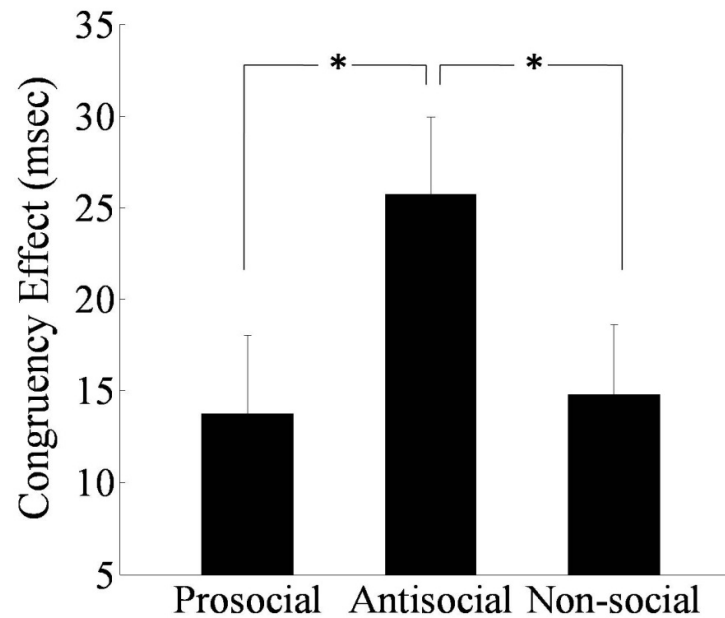
RT (msec)	Prosocial	Antisocial	Non-social
Congruent trials	427 *(29.9)*	429 *(36.5)*	430 *(29.0)*
Incongruent trials	441 *(29.0)*	455 *(35.6)*	445 *(27.5)*
Baseline trials	434 *(31.9)*	436 *(32.5)*	437 *(34.6)*

Figure 6-2. (a) Mean Congruency Effect for the three types of priming (prosocial antisocial and non-social). Asterisks represent the statistically significant difference between two bars. Vertical bars indicate standard error. (b) Mean Reaction Time in milliseconds (msecs) for participants in each of the three priming groups on congruent, incongruent and baseline trials. Italic numbers indicate standard error.

6.4 Experiment 2: Does self-relatedness play an important role in the priming effect on mimicry?

Experiment 1 provided the initial evidence that priming antisocial behaviors enhances mimicry. People showed a stronger tendency to mimic following antisocial priming than prosocial and non-social priming (Figure 6-2a). This result is compatible with previous studies of the impact of ostracism priming on mimicry (Lakin et al., 2008; Over and Carpenter, 2009a). However, the results contradict the very similar study by Leighton et al. (2010), which found stronger mimicry following prosocial priming in the same task.

One key difference between our study and that of Leighton lies in the priming sentences themselves. Our priming stimuli in experiment one provided examples of antisocial behavior conducted by two particular characters (e.g. 'Paul helps Ivy to fix her old bicycle', 'Jane and William dispute the money they earn'). In contrast, Leighton's priming stimuli used more abstract and self-related sentences (e.g. 'She is my friend', 'We are against this'). According to Dijksterhuis' theory (2001) that the self-relatedness plays a key role in the process of social priming, it is likely that different self-relatedness between Leighton's priming sentences and ours leads to the opposite priming results on mimicry.

In order to test this idea, we produced two new sets of scrambled sentences in Experiment 2: one was to describe the pro/anti social behaviors from a third person's perspective, just like experiment 1 (e.g. 'Greg encourages others to be friends with Lauren', 'Joe cruelly bullied Stephanie about her weight problem'), and the other was to modify the same priming

sentences from a first person's perspective (e.g. 'We encourage others to be friends with Lauren', 'I cruelly bullied Stephanie about her weight problem'). All the pro/antisocial behaviors in the first-person and third-person perspective version were identical, except that the former were self-related and the latter were not. As previous studies suggest that perspective taking influences priming effects on automatic behavior (Wheeler et al., 2001), we hypothesized that this modulation applies to mimicry as well. Specifically, we predicted that the third-person perspective group would replicate Experiment 1's results and the first-person perspective group would replicate Leighton's.

6.4.1 Methods and Materials

Participants

Thirty-two undergraduate students (18 females and 14 males; average age 21.8; S.D. 2.03 years) participated in this study. None of them had participated in Experiment 1. Half of the participants (9 females and 7 males) were randomly assigned to the 3rd person perspective group, the other half to the 1st person perspective group.

Stimuli, design and procedure

These were the same as those in Experiment 1, except that two new sets of scrambled-sentence task were prepared for each perspective-taking group. For the third person perspective group ('non self-related'), 12 pages of new scrambled sentences were remade: 4 pages of prosocial behavior priming (e.g., 'Harrison helps Julie to understand difficult maths problems', 'Greg encourages others to be friends with Lauren'), 4 pages of antisocial behavior priming (e.g., 'Joe cruelly bullied Stephanie about her weight problem' , 'Pippa

challenged Jack to a fight after school') and 4 pages of non-social priming (e.g., 'Yorkshire pudding and horseradish go with roast beef', 'There are 366 days in each leap year'). For the first person perspective group ('self-related'), we adopted the same sentences but just changed the first character's name into "I" or "we", for example: first-person prosocial behavior priming (e.g., 'I help Julie to understand difficult maths problems', 'I encourages others to be friends with Lauren') and first person antisocial behavior priming (e.g., 'I cruelly bullied Stephanie about her weight problem' , 'I challenged Jack to a fight after school'). The non-social priming sentences in first and third person group were the same.

6.4.2 Results and Discussion

The same procedure as Experiment 1 was implemented on raw RT data, to remove incorrect responses (0.03%) and RT outliers (0.10%).

First, in order to examine whether self-relatedness can affect the priming effects on mimicry, a three-way repeated measures ANOVA was conducted on participants' mean RT, with congruency (congruent, incongruent, baseline), primes (prosocial, antisocial, non-social) and self-relatedness (3rd-person, 1st-person) as variables. The three-way ANOVA analysis revealed a significant main effect of congruency ($F_{(2,60)}=48.64$, $p<0.001$) and a significant three-way interaction: congruency × primes × self-relatedness ($F_{(4,120)}=2.59$, $p<0.040$). We also performed a two-way ANOVA on participants' CE with primes (prosocial, antisocial, non-social) and self-relatedness (3rd-person, 1st-person) as variables. In line with the three-way interaction on RT, the two-way ANOVA analysis revealed a significant two-way interaction on CE: primes × self-

relatedness ($F_{(2,60)}=4.56$, $p<0.014$). These results suggest that the priming effects on mimicry between two perspective-taking groups were different.

In order to further examine the specific priming effect on mimicry in each perspective-taking group, we independently conducted a repeated measures ANOVA analysis for each group, on mean CE with primes (prosocial, antisocial, non-social) as variables (Figure 6-3). The analysis revealed a significant main effect of primes on CE in both 3rd-person ($F_{(2,30)}=4.962$, $p<0.014$) and 1st-person ($F_{(2,30)}=3.58$, $p<0.040$) group. For 3rd-person group, post-hoc t-test showed that the CE in antisocial priming condition was significantly larger than the one in prosocial ($t_{(15)} = 2.48$, $p<0.025$) and non-social ($t_{(15)} = 3.25$, $p<0.005$) priming condition, which replicated the results in experiment 1. On the contrary, post-hoc t-test in 1st-person group showed that CE in antisocial priming condition was significantly smaller than the one in prosocial priming condition ($t_{(15)} = 2.32$, $p<0.035$), which was compatible with the findings of Leighton and colleagues (2010).

Taken together, the results in 3rd person group replicated experiment one with a new group of participants; and the results in 1st person group replicated Leighton's findings in the context of our experimental task. Antisocial behavior primes enhance mimicry only in the 3rd-person group whereas prosocial behavior primes enhance mimicry only in the 1st-person group. These results suggest that the self-relatedness of a pro/antisocial prime is crucial for its specific priming effect on mimicry.
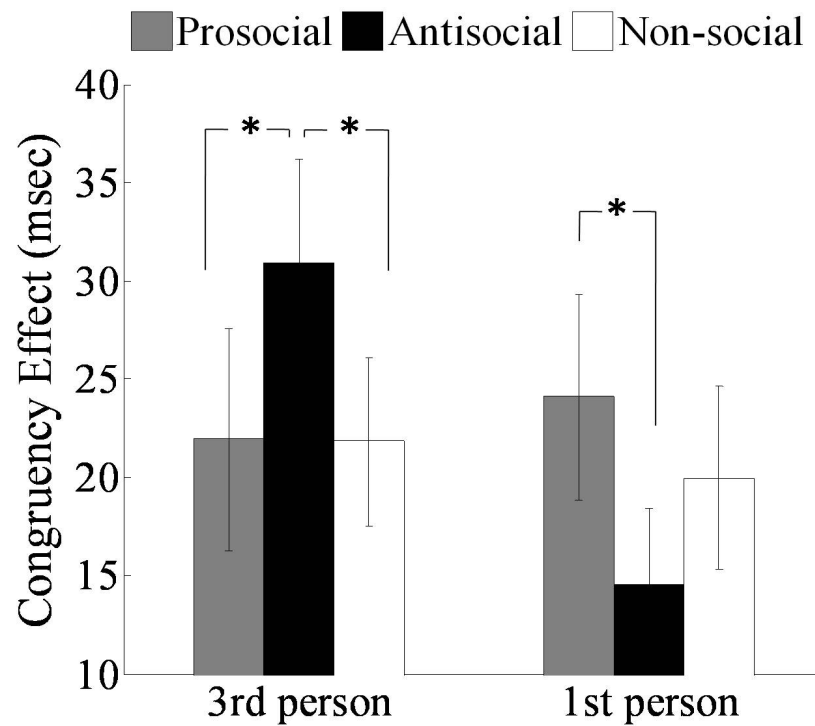
Figure 6-3. Mean CE for the three types of social behavior priming (prosocial, antisocial and non-social) in two perspective-taking groups (3rd person and 1st person). Asterisks represent the statistically significant difference between two bars. Vertical bars indicate standard error.

6.5 General Discussion

In the present study, we tested the relationship between pro/antisocial priming and mimicry. Given the past literature showing that both prosocial and antisocial primes can enhance mimicry, we predicted that self-relatedness of primes is important in understanding these mixed priming effects on mimicry. This prediction was confirmed in two experiments. In Experiment 1, we demonstrate that pro/anti social behavior priming has an impact on mimicry in the context of our experimental task and priming antisocial behavior by a third party leads to increased mimicry. Experiment 2 replicated this effect, but also demonstrates that priming similar antisocial behaviors by the self leads to decreased mimicry. These results provide direct evidence that self-relatedness plays an important role in the priming effects on mimicry.

The crucial question then concerns the underlying mechanisms of how priming antisocial behavior leads to increased mimicry and how the self-relatedness of a prime alters its priming effect on mimicry. One possibility is that when participants received antisocial primes by a third-person, they strategically used mimicry to enhance social cohesion (Over and Carpenter, 2009a) whereas when they received antisocial primes by the self, they strategically reduced mimicry to sustain social disharmony. This interpretation is compatible with our results in Chapter 5 where we showed that mimicry is strategically controlled by social signals. According to this interpretation, perception of antisocial behavior from the third-person perspective might act as a hint of disaffiliation (Over and Carpenter, 2009a). This could increase participants' prosocial motivation, presumably in an attempt to stop the social

conflicts and recover social affiliation, which in turn increases their tendency to mimic others. This could also explain why prosocial primes by a third-party do not enhance mimicry, simply because a hint of harmony from other's prosocial behavior informs participants of no need to implement more mimicry to create social cohesion. In contrast, priming antisocial behavior from the first-person perspective might act as a goal of disaffiliation, an attempt to implement and fulfill these antisocial behaviors, which doubtlessly decreases their overall mimicry.

Another plausible theory could be derived from the stereotypic behavior priming study by Dijksterhuis and colleagues (Dijksterhuis et al., 1998). They found that stereotypic behavior priming can induce two contrasting effects on automatic behavior: 'behavioral assimilation' and 'behavioral contrast'. The former elicits stereotype-consistent behaviors and the latter elicits stereotype-inconsistent ones. Several factors have been identified so far to determine the direction of the effect a prime leads to, and they are all associated with implicit self-relevant process. For example, primes with abstract and generalized stereotypic concepts or presented from the first-person perspective increases accessibility to 'behavior assimilation' whereas primes with concrete and extreme stereotypic exemplars or presented from the third-person perspective increases accessibility to 'behavior contrast' (Dijksterhuis et al., 2001; Wheeler et al., 2001). Following this logic, it is possible that the primes in the first-person perspective might result in more "behavioral assimilation" and consequently the prosocial primes will elicit more prosocial-consistent behaviors such as mimicry; in contrast, the primes in a third-person perspective might lead to more "behavioral contrast" and as a result the

antisocial priming reversely induces more prosocial mimicry behaviors. This behavioral assimilation and contrast mechanism can not only help us better understand the mixed results in the previous mimicry priming literature, but also extend Dijksterhuis' theory from stereotypic behavior domain to other automatic behavior domains such as mimicry.

Our results also have important methodological implications for future priming research on mimicry. Leighton et al. (2010) found that a priming sentence enhances mimicry when it contains prosocial words and inhibits mimicry when it contains antisocial words. However, by using the same task, our results revealed that priming sentences with prosocial behavior enhance mimicry only in the first-person perspective group and priming sentences with antisocial behaviors inhibit mimicry only in the third-person perspective (Figure 6-3). This suggests that mimicry is not only sensitive to the pro/antisocial words in the priming sentences, but also the perspective of the sentences. Studies using tasks like the scrambled sentences task to provide conceptual priming must thus consider the whole meaning of each sentence, not just the presence of key pro/antisocial words.

Finally, it might be interesting to discuss the possible neural mechanism for the pro/anti social priming effects on mimicry. Past research suggests that medial prefrontal cortex (mPFC) is an important brain region for the control of mimicry (Brass et al., 2001a, 2005, 2009). Chapter 4 demonstrated that social stimuli such as eye gaze modulate mimicry by influencing the neural activity in mPFC. mPFC is also strongly involved in self-related task (Amodio and Frith, 2006). For example, implicit self-other evaluation and comparison strongly engage mPFC (Moran et al., 2009; Rameson et al., 2010). Moreover, mPFC

has been linked to one's prosociality. Activity in mPFC was found to be correlated with daily prosocial behavior (Rameson et al., 2011) and more activities in mPFC predicted more subsequent prosocial behavior toward a rejection victim (Masten et al., 2011). Interestingly, a recent neuroimaging study suggests that mPFC is also the neural substrate for social priming effects on behavior. Bengtsson et al., (2011) showed that mPFC is actively engaged when self-esteem primes modulate one's cognitive monitoring ability. Given the fact that mPFC involves in all four processes of social priming, control of mimicry, prosociality and self-relatedness, it appears likely that processing of the prosociality and self-relatedness of a prime takes place in mPFC and the neural activity of mPFC determines the pro/antisocial priming effects on mimicry. Future research could investigate this.

6.6 Conclusion

In sum, the present study clarifies the relationship between pro/anti social primes and mimicry and revealed the importance of self-relatedness in the priming effects on mimicry. Two experiments consistently showed that priming antisocial behavior by a third party leads to increased mimicry but priming it by the self leads to decreased mimicry. This means that how mimicry is primed depends on both the prosociality and self-relatedness of the priming stimuli. Future research can investigate how this subtle modulation is implemented.

Chapter 7. Discussion

7.1 Summary of Experimental results

This thesis uses both behavioural and brain imaging techniques to investigate the control of mimicry by social signals. The results presented here demonstrate that mimicry is subtly and strategically controlled by social signals, and suggest that this strategic control of mimicry contributes to human competence in social interaction.

Chapter 2 investigated whether eye gaze can modulate mimicry on a second by second timescale, and found that direct gaze rapidly and specifically enhances mimicry of intransitive hand actions. Chapter 3 replicated this enhancement effect by using a novel gaze sequence paradigm and further demonstrated that the eye contact effect on mimicry is not based on any arousal or attentional effects. Importantly, our results suggested that the enhancement of mimicry is strategically driven by the ostensive-communicative nature of the direct gaze. These findings reflect the flexibility and subtlety of mimicry in social contexts and also suggest that eye gaze is a powerful and strategic controlling signal on mimicry.

Chapter 4 investigated the neural mechanism of the eye contact effect on mimicry by using fMRI. The results showed two key brain systems for social cognition—mPFC and MNS—work together to on-line control mimicry in social contexts. In particular, DCM analysis revealed that mPFC is the originator of the eye contact effect on mimicry and it modulates the sensory inputs to the MNS according to gaze directions. These findings suggest that mPFC plays a

key role in the strategic control of mimicry in social contexts.

Chapter 5 investigated the joint effect of two critical features—likeability and social status—on mimicry and examined if mimicry is simply driven by the summation of the two features or is more sophisticatedly driven by the affiliative function of mimicry. The results showed a significant interaction between social status and likeability in driving mimicry and this interaction optimized the affiliative function of mimicry in social interaction. This supports a strategic nature of mimicry where participants used mimicry as a communicative tool to affiliate with others. These findings, along with the ones in Chapter 3, provide convincing evidence that mimicry is strategically controlled by social signals.

Chapter 6 investigated the relationship between pro/antisocial priming and mimicry. Previous studies showed a mixed data where antisocial priming can both enhance and inhibit mimicry. Here, two experiments consistently showed that priming antisocial behavior by a third party leads to increased mimicry while priming antisocial behavior by the self leads to decreased mimicry. These results suggest an important role of the self-relatedness in the effects of social priming on mimicry, and also reflect the strategic nature of mimicry, that is, people strategically increase mimicry to change the antisocial surroundings.

7.2 Emerging Questions

In most research, finding an answer to one question brings about several more questions, and this work is no exception. As well as the strategic control of mimicry by social signals was found in this thesis, these findings have several general implications for our understanding of how and why we mimic in the real social world, which will be considered below.

7.2.1 How Do We Mimic in the Real Social World?

The studies in this thesis suggest that mimicry is subtly and strategically controlled by social signals and this control of mimicry is mediated by mPFC. However, these studies were conducted under very simple lab conditions where the type, onset and frequency of a social signal are well-controlled. It should be more complicated in the real social world where multiple social signals simultaneously jump into our visual field. Then, how would the brain dynamically control mimicry according to different social signals?

When we watch an actor performing an action, we perceive not only the action itself, but also the social signals along with the action (Figure 7-1). These social signals can be divided into three groups: rapid changing signals such as ostensive signals (e.g. eye gaze and smiles), occasional signals about the social contexts (e.g. social ostracism, recent failure to affiliate with others) and fixed signals such as personal characteristics (e.g. social status and membership). I argue that in the temporal domain, these three different types of social signals modulate mimicry in different fashions. First, I claim that the fixed social signals such as a person's characteristics strategically determine the long-term baseline of the magnitude of mimicry towards that

person. Take the Queen's photo in Figure 7-1 as an example, merely from the appearance we can recognize her social status (high status), likeability (graceful) and membership (Caucasian, Christian, Elders). These fixed features were then processed to determine whether there is a need to affiliate with her (Yes! because of high status) and to estimate how much mimicry is needed to successfully affiliate with her (perhaps intermediate amount of mimicry, because she is too nice, see chapter 5).

Second, I suggest that the occasional social signals such as social contexts strategically determine the short-term baseline of the magnitude of mimicry to others. Lakin and Chartrand (2003) and Lakin et al., (2008) found that those with a recent failure to affiliate with others or those with a recent experience of social ostracism showed short-term increased mimicry to others. The results in Chapter 6 also found that participants who were primed by other's antisocial behaviour displayed more mimicry. These findings suggest that when people were surrounded by a disharmony social context, they estimate a strong need to affiliate with others in the near future and therefore strategically heighten the baseline of the magnitude of mimicry for a short period.
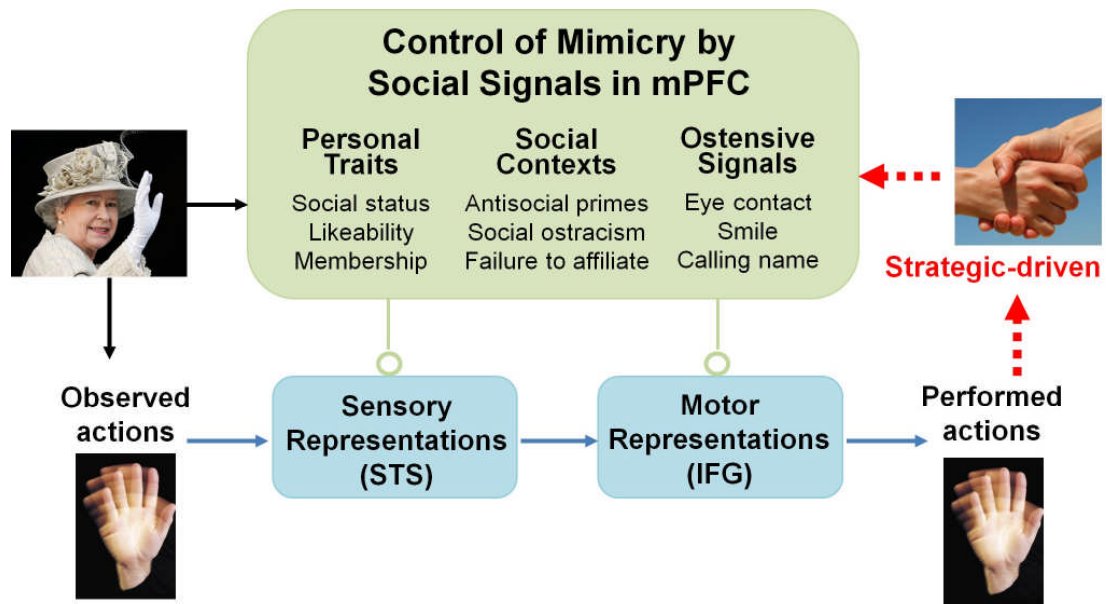
Figure 7-1. A dynamic model for strategic mimicry. This figure illustrates how mimicry is dynamically controlled by social signals. The photo of the Queen and black arrows symbolize the perception of a target performing a movement; this scene not only activates the processes of action perception, but also triggers the processes of social signals. The blue boxes and arrows represent the process of mimicry where the sensory information of the observed action is transformed into the motor plan of that action. This process is mediated by the core MNS such as IFG (motor representations) and STS (sensory representations). The green boxes and lines represent the strategic control of mimicry by social signals. The works in this thesis provide evidence that mimicry is subject to strategic top-down control processes by social signals (green boxes and lines), for example, based on the fixed characteristics of the target (e.g. social status), or based on the occasional social contexts (e.g. social ostracism) or based on the rapid changing ostensive cues given by the target (e.g. eye contact). These top-down modulation processes could act at either the sensory input or motor output of the mimicry process to reduce or enhance mimicry. The hand shaking photo and red arrows symbolize the strategic-driven nature of mimicry where mimicry is used to enhance interpersonal relationship. How much the social signals enhance or

inhibit mimicry process depends on the estimation of the current need to affiliate with that actor. If there is a strong need to affiliate with the actor (e.g. high social status such as the Queen), the control system would strategically increase more mimicry.

Third, I suggest that the rapid changing signals such as ostensive signals strategically determine the current magnitude of mimicry to the signal sender. In chapter 2 and chapter 3, we found that direct gaze rapidly and strategically enhances one's tendency to mimic. Therefore, in the example of the Queen's photo (Figure 7-1), her eye contact and communicative smile would elicit increased mimicry to her. However, she might not always send the same signals, for example, in the next moment, she might show an averted gaze and unhappy face. This rapid change of ostensive signals would then subtly modulate the perceiver's estimation of the current need to affiliate with the gaze sender and consequently impact the magnitude of mimicry in a second-by-second scale.

Finally, I suggest that in the real social world, the overall magnitude of mimicry towards a target is the summation of the strategic mimicry by these three types of social signals. The mPFC dynamically receives these social signals along with the action from the target and consequently estimates the current need of strategic mimicry. Subsequently, mPFC exerts top-down modulation on the sensory input or motor output of the mimicry process to reduce or enhance mimicry (chapter 4).

7.2.2 The Relationship between Mimicry Effect and Visible Mimicry Behaviour

As I reviewed in the introduction chapter, research in social psychology mainly focuses on visible mimicry behaviours (e.g. face touching and foot shaking in 'the Chameleon effect') whereas research in cognitive neuroscience primarily investigates the underlying mimicry effect (e.g. RT congruency effect and mirroring mechanism in MNS). However, what is the relationship between mimicry effect and visible mimicry behaviours? It is widely believed that mimicry effect is the neural mechanism of visible mimicry behaviours (see 1.2.7). But since observing an action automatically triggers the tendency to execute that action, why does not every mimicry effect turns into a visible mimicry behaviour? For example, participants show a significant mimicry effect in all SRC tasks in this thesis, but they showed few erroneous movements (i.e. error rate), which can be regarded as a visible mimicry behaviour.

It is difficult to directly answer this question because the generation of a visible behaviour depends on the complex competition between excitatory and inhibitory systems (or factors) of that behaviour. From this point of view, mimicry effect could be regarded as the excitatory system of visible mimicry behaviour, because the mirroring mechanism excites the motor system for that action (see 1.2.3 Fadiga's effect). Social modulators such as the motivation to affiliate, prosocial attitude, positive mood, high social status and ingroup membership (see 1.1.5) are excitatory factors for visible mimicry behaviour, because previous studies showed that they increases spontaneous

mimicry behaviour during interactions. In addition to these, this thesis suggests that social signals such as direct gaze (chapter 2) and communicative gaze sequences (chapter 3) could also be included as the excitatory factors for visible mimicry behaviour, because they directly enhance MNS (chapter 4).

For the inhibitory system of mimicry behaviour, previous studies suggest that mPFC is the neural substrate of the inhibition of mimicry (Brass et al., 2001; 2005). Incongruent actions engage more mPFC activity than congruent actions in healthy participants, and difficulties in the inhibition of mimicry have been observed in patients with lesions in mPFC (see 1.2.7). Past studies also suggest several inhibitory factors for mimicry. For example, social stigma, negative mood, low social status and outgroup membership significantly reduce one's spontaneous mimicry behaviour in social interactions. In addition to these, this thesis found that nasty personality with low status (chapter 5) and priming an antisocial behaviour by the self (chapter 6) are two social factors that inhibit mimicry.

Here I would like to point out another critical factor that has strong effects on the inhibition system of mimicry—the self-focus. Previous studies found that increasing self-focus significantly decreases mimicry. For example, Provine and colleagues (1986) found robust effects for contagious yawning when participants were exposed to videos of people yawning; however when the participants explicitly knew they were being watched during the experiment, the contagious yawning disappeared (Provine, 2005). This supports the idea that spontaneous mimicry behaviour can be suppressed by conscious self-awareness. Similar effects by the self-focus were also found on

mimicry effect. Spengler et al., (2010c) manipulated participants' self-focus by either using an optical mirror or using a self-evaluation task. They found that when participants can see their own image from the mirror or had been asked to make judgments about themselves, less mimicry effect was observed in the SRC tasks. The authors explained that because mPFC, as the neural substrate of inhibition of mimicry, is also a critical brain region for self-referential process, increasing self-focus inevitably activates mPFC and thus suppresses mimicry.

This inhibitory effect of self-focus on mimicry can help us explain some situations where mimicry effect fails to generate a visible mimicry behaviour. For example, the observation that people exhibit less visible mimicry behaviours (i.e. erroneous finger/hand movements) in the SRC paradigm than natural setting paradigm could result from the experimental instructions provided, because the instructions of SRC paradigms often direct participants to the awareness of self-performance (e.g. 'as fast and accurate as you can') while the natural setting paradigms require participants to focus on the side of the interaction partner (e.g. 'describe this photo to your partner').

In sum, although mimicry effect is the neural mechanism of visible mimicry behaviour, it is obviously that the former would not always lead to the latter. In real social world, many excitatory and inhibitory factors jointly influence the MNS and mPFC. Future research is needed to investigate how these factors are computed and weighted in the generation of a visible mimicry behaviour.

7.2.3 Why Do We Mimic in the Real Social World?

Four models of why people mimic

A core question in mimicry research is to clarify why people mimic. Four different models have been proposed so far (see 1.1.6 and 1.2.6).

1) *Innate model.* This model suggests that mimicry is innate or at least based on some amount of genetic predisposition at the neuron level (Lepage and Théoret, 2007). It claims that mimicry is evolutionarily favored and selected, because it involves important social functions such as social affiliation (Lakin et al., 2003), action understanding (Rizzolatti and Craighero, 2004) and learning through observation (Buccino et al., 2004).

2) *Simulation model.* This theory claims that mimicry is part of the fundamental simulation mechanism of the brain. It helps people understand other's behaviours and gives people better insight into other's mental states (intentions and desires) (Niedenthal et al., 2010). People mimic others because they have to understand others.

3) *ASL model.* This model claims that mimicry is not evolutionarily selected for any specific function, but is a byproduct of associative learning processes (Heyes, 2001; 2010; see 1.2.7). As generated by domain-general processes, once established, mimicry might be involved in several general adaptive functions such as imitative behaviour, action understanding and social affiliation (Brass and Heyes, 2005).

4) *Strategic model.* This theory claims that mimicry is a strategic nonverbal behaviour to enhance liking and affiliation between individuals.

A person mimicking other is because he/she wants to change the social world for self-advantage—being liked and affiliated by others. Thus the cause of mimicry is for maintaining a successful interpersonal relationship (Lakin et al, 2003).

These four models share both similarities and discrepancies. For example, the innate model suggests that mimicry is innate while the ASL model suggests that mimicry is formed by associative learning during development. The innate model, simulation model and strategic model propose that mimicry is responsible for a specific social function while the ASL model propose that mimicry involves in several general adaptive functions.

Several hybrid theories have already been proposed. For example, Del Giudice et al.,(2009) combined elements of the innate model and ASL models, and proposed that mimicry comes from the synergistic effect of associative learning and genetic pre-programmes advantageous for this learning. They claim that because mimicry is involved in important social functions, evolution optimized infant behavioural patterns to produce efficient and reliable associative learning for mimicry in the brain.

Our data for these models

The main purpose of my PhD project is not to verify these models; however, some findings from this thesis can provide insights for our understanding of these models. For example, in all experimental chapters we found that mimicry is subtly modulated by social signals. If mimicry is innately selected for action understanding (the 'innate model'), there is no need to be sensitive to different gaze directions (chapter 2) or be modulated by different

gaze sequences (chapter 3), because the action type (hand opening/closing movements) remained identical whenever it was preceded by a direct/averted gaze or a communicative/non-communicative gaze sequence. Similarly, if mimicry is part of a fundamental simulation mechanism for understanding other's actions and mental states (the 'simulation theory'), it will be difficult to understand why mimicry was significantly decreased by low status and nasty personality (chapter 5), because we still need to simulate and understand the actions performed by people with these traits.

Our results from chapter 4 and chapter 5 support part of the ASL theory. The ASL theory stresses on the uniqueness of sensorimotor experience to the formation of mimicry (Heyes, 2010, see 1.2.6). It claims that only the sensorimotor experience can directly interfere with the vertical association between the sensory and motor representation of an action; any other modulations of mimicry are mediated by either influencing the sensory component or the motor component of the vertical association (Catmur et al., 2009). Our DCM analysis in chapter 4 showed that under different social gazes, the mPFC enhances mimicry by modulating the sensory input to the MNS. In contrast, the results in chapter 5 suggest that social status and likeability drive mimicry by modulating the inhibition of mimicry, which is the motor output of the sensorimotor mapping. These data are compatible with the ASL model which suggests mimicry can be modulated by changing either input to or output from the MNS but not changing the sensorimotor mapping.

The findings in all experimental chapters support the strategic account of mimicry. We found that people strategically increased mimicry when there was a cue or need for social affiliation, such as direct gaze (chapter 2),

communicative gaze sequence (chapter 3), nasty target with high social status (chapter 5) and antisocial behaviours (chapter 6). This strategic nature of mimicry implies that mimicry specifically devotes to social affiliation.
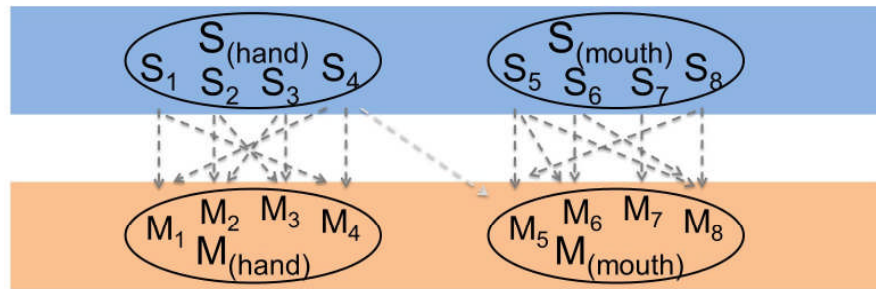
Social cohesion model

Motivated by the findings in this thesis, here I propose a new hybrid theory—'social cohesion model', which combines elements of the innate model, ASL model and strategic model. Basically, it claims that because people have a fundamental and pervasive drive to affiliate with others (Baumeister and Leary, 1995), evolution selects mimicry as a strategic tool to satisfy one's need of social cohesion. Specifically, I adopt the claims in the innate model suggesting that mimicry is evolutionarily selected for a specific social function and propose that mimicry is for social cohesion. I also adopt the claims in the ASL model suggesting that mimicry is formed by sensorimotor experiences, and further propose that sensorimotor experiences are facilitated by some genetic predisposition for social cohesion. Finally, I adopt the claims in the strategic models suggesting that mimicry is a strategic tool to enhance social cohesion and propose that the control of mimicry by social signals is to optimize the affiliative function of mimicry.

This 'social cohesion model' suggests that human mimicry is not innate, but originates from some genetically-wired mimicry-like mechanisms, such as action synchronization. As I mentioned in 1.1.2, migrating fishes and birds display impressive synchrony of movement; similarly, synchronization of voices is a typical behaviour in many collective animals (e.g. birds, wolves and non-human primates). These primitive synchronized behaviours are innately reflexive and are believed to be evolutionarily selected as an essential survival

skill for social cohesion (Breder and Halpern, 1946; Conradt and Roper, 2000; Aivaz and Ruchstuhl, 2011). However, the neural mechanism of action synchrony is still unknown.

By considering that action synchrony is a primitive and rudimentary type of mimicry where the seeing and doing behaviours are not perfectly matched but always performed by the same effectors, the 'social cohesion model' suggests that associations between sensory and motor representations are imbalanced at birth (Figure 7-2a). Sensory neurons would have stronger associations with motor neurons when they code the same effector's actions than different effector's actions. For example, a sensory neuron of mouth movements (e.g. an open mouth) would have a stronger default association with a motor neuron of mouth movements (e.g. mouth opening) than a motor neuron of hand movements (e.g. hand stretching). These stronger default associations for the same effector's actions are accumulated by the habits of action synchrony in the history of evolution and are specifically selected for social coordination and affiliation. In contrast, when it comes to the same effector system, the sensory neurons and motor neurons are unsystematically, randomly connected (similar to the ASL model, see Heyes, 2010) (Figure 7-2). For example, the sensory neuron of mouth opening could be equally connected to motor neurons of mouth opening and lip protrusion. The 'social cohesion model' suggests that these imbalanced default associations have no social function in infants because the associations between sensory and motor representations are non-specific, but they provide an evolutionarily favored neural pattern for social cohesion and will be further optimized by sensorimotor experiences and social control system.

A. Primitive action synchrony at birth

B. Mature mirroring mechanism after sensorimotor experience
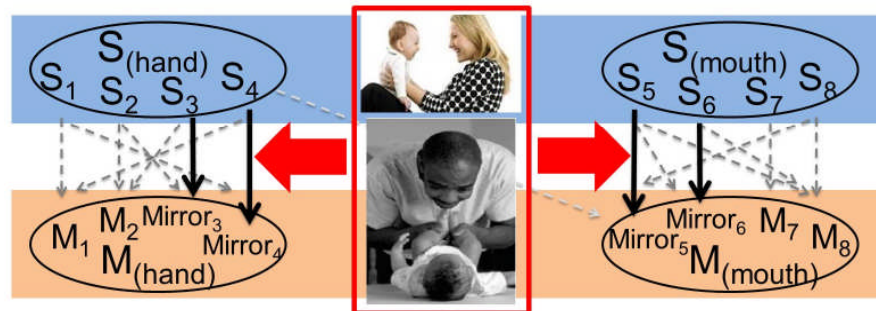
C. Strategic mimicry
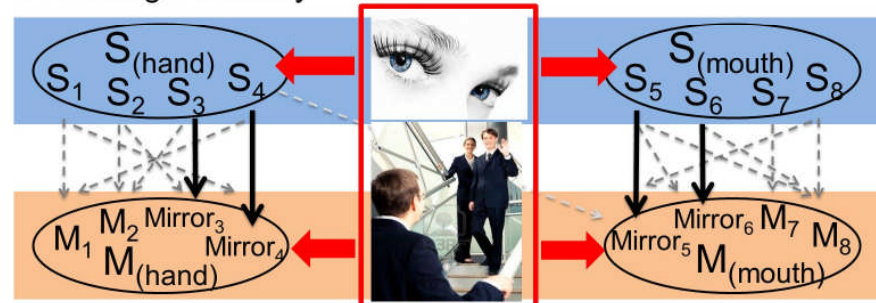
Figure 7-2. The 'social cohesion model' of mimicry (modified from Heyes, 2010). (A) Mimicry origins from a rudimentary neural system for primitive action synchrony. This system is featured by imbalanced associations between sensory neurons in STS (blue) and motor neurons in IFG (orange). Sensorimotor associations are stronger within the same effector system than between different effector systems. (B) Mature mirroring mechanism is developed by sensorimotor experiences, which elaborately specify the associations between sensory neurons and motor neurons. Ostensive signals such as eye contact facilitate the associative learning during sensorimotor experiences. (C) Mimicry is strategically controlled by social signals such as eye contact and social status. These signals

influence either the sensory input or the motor output of the sensorimotor mapping, in order to optimize the affiliative function of mimicry.

Similar to the ASL model, the 'social cohesion model' suggests that a mature, functional neural mechanism for mimicry is developed by sensorimotor experiences, which elaborately specifies the vertical association between sensory neurons and motor neurons. However, the 'social cohesion model' further suggests that the efficient and reliable associative learning during sensorimotor experiences is promoted by some amount of genetic predisposition for social cohesion, for example, the sensitivity to ostensive signals. Ostensive signals are special social signals that human being evolved to facilitate social interaction and cooperation (Frith and Frith, 2010). Ostensive signals such as eye contact, eyebrow raise and calling name convey communication intention and ultimately promote social affiliation. Ostensive signals also play an important role in infant's development (Csibra and Gergely, 2009). Eye contact and infant-directed speech ('motherese') attract infants' attention (Senju and Csibra, 2008) and facilitate their social learning from others (Csibra and Gergely, 2006, 2009). The 'social cohesion model' suggests that these ostensive signals are important for effective associative learning from sensorimotor experiences, because they assure that the established sensorimotor mappings are social-cohesion-oriented.

The claim that ostensive signals are important to the development of functional mimicry is supported by several studies. According to the ASL model, self-observation (often without ostensive signals) contributes to the most infants' sensorimotor experiences (Heyes, 2010). However, several

studies suggests that most of human spontaneous mimicry during fact to face interaction are 'mirror mimicry' (i.e. interaction partners move the hand on the same side), not 'anatomic mimicry' (e.g. interaction partners move the same hand) (Bavelas et al. 1988; LaFrance and Broadbent, 1976). The neural activities of MNS are also stronger during mirror mimicry than during anatomic mimicry (Koski, et al., 2003). This preference of mirror mimicry implies that the associative learning during self-observation would be modified or replaced by the associative learning during the existence of ostensive signals, because the latter one optimizes the social cohesion function of mimicry (i.e. mirror mimicry facilitates social coordination and cooperation). Future research needs to verify this claim.

The final claim of the 'social cohesion model' is that all modulations of mimicry by social signals are to optimize the affiliative function of mimicry. It argues that the associative learning is a domain-general process which could produce some rigid, non-adaptive mimicry response. As the function of mimicry is for social cohesion, human develops monitoring mechanisms which strategically control the sensory input or motor output of mimicry according to contexts, to assure and maximize its affiliative consequence. The experimental results in this thesis confirm this idea and suggest that the control of mimicry by social signals is in a Machiavellian fashion. For example, social signals such as eye contact (chapter 2 and chapter 3), social status (chapter 5) and social primes (chapter 6) strategically modulate mimicry to maximize the affiliative consequence of mimicry. These sophisticated controls of mimicry cannot be simply explained by the innate model and simulation model. Moreover, previous studies suggest a strong animacy bias of

mimicry—people display more mimicry to a biological movement when they were told the movements were performed by a human agent than they were told the movements were performed by an artificial device (Liepelt and Brass, 2010; Longo et al. 2008; see 1.2.5). It will be difficult for the ASL model to explain why the belief about animacy modulates mimicry, because the low-level perceptual features (i.e. sensory input) of the movement remain identical in these studies and they should elicit the same motor response in the ASL framework. The 'social cohesion' model attributes this animacy bias to the 'strategy for social cohesion. It suggests that because the function of mimicry is to satisfy human's need for social cohesion, there is no need to strategically use mimicry to affiliate with any artificial devices.

In sum, the 'social cohesion' model suggests that mimicry is evolutionarily selected for social cohesion. It is not innate, but gradually developed with the assistance of genetic predisposition for social cohesion. It origins from a rudimentary neural system for primitive action synchrony and is elaborately developed by associative learning process during sensorimotor experiences. Finally, mimicry is strategically controlled by social signals to optimize its function of social cohesion. While the 'social cohesion model' is admittedly speculative and cannot totally rule out the possibility that the control of mimicry by social signals is mediated by domain-general processes such as attention, I argue that this new model has two distinct advantages: it goes beyond simple nature–nurture dichotomies and is consistent with current evolutionary biology; and it adopts the pros of previous models and is strongly supported by the experimental results in this thesis.

7.2.4 Mimicry in Autism

Finally, the results in this thesis may have implications for our understanding of mimicry in autism. Autism is a neurodevelopmental disorder characterized by abnormalities of social interaction and impairments in communication. A number of studies have demonstrated reduced mimicry and MNS activity in individuals with autism compared to control participants (Williams et al. 2004; Dapretto et al. 2006; McIntosh et al. 2006; Oberman et al. 2005; Rogers et al. 2003; Stel et al., 2008). It has been hypothesized that a 'broken MNS' and corresponding mimicry impairment is a core feature of autism (Williams et al. 2001). However, the experimental evidence for this theory is highly controversial. Increasing studies in recent years suggest that mimicry remains intact in autism (Bird et al. 2007; Dinstein et al. 2010; Gowen et al. 2008; Hamilton et al. 2007; Leighton et al. 2008; Press et al. 2010; Spengler et al. 2010b).

Instead of suggesting impairment in mimicry per se, Hamilton (2008) recently proposed that individuals with autism might have impaired control of mimicry. This theory is compatible with clinical observations of high levels of echolalia (automatic repetition of speech patterns) and echopraxia (automatic imitation of observed actions) in autistic patients where they cannot inhibit excessive vocal and action mimicry (Russell 1997; Rutter 1974). Our findings in this thesis suggest that the strategic control of mimicry by social signals is essential to the function of mimicry. Subtly and strategically controlling mimicry according to social contexts optimizes the affiliative consequence of mimicry and contributes to human competence in social interaction. As individuals with autism have severe deficit of social perception (e.g. eye

contact) and impaired competence in social interaction, it is possible that the strategic control of mimicry by social signals is compromised in autism. Future research is needed to verify this theory.

7.3 Overall Conclusion

In conclusion, the experiments presented in this thesis demonstrate that mimicry is flexible and sensitive to social contexts. Social signals such as eye gaze, social status, likeability and pro/antisocial primes subtly and strategically control mimicry, in order to optimize the affiliative consequence of mimicry. Neuroimaing data suggest that mPFC plays a key role in the control of mimicry by social signals; it works together with MNS to on-line control mimicry according to social contexts. These findings reflect the strategic nature of mimicry and provide important implications for our understanding of the causes and functions of mimicry.

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