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Cognitive mechanisms for responding to mimicry from others

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Highlights

- We review evidence for the downstream effects of being mimicked
- Effects such as liking are fragile and modulated across context and individuals
- Neural effects have been found in mirroring, reward and self-other regions
- We outline models involving self-other overlap, contingency or predictive coding
- Mimicry priming and virtual mimicry may provide useful future paradigms

Abstract

Compared to our understanding of neurocognitive processes involved producing mimicry, the downstream consequences of being mimicked are less clear. A wide variety of positive consequences of mimicry, such as liking and helping, have been reported in behavioural research. However, an in-depth review suggests the link from mimicry to liking and other positive outcomes may be fragile. Positive responses to mimicry can break down due to individual factors and social situations where mimicry may be unexpected. It remains unclear how the complex behavioural effects of mimicry relate to neural systems which respond to being mimicked. Mimicry activates regions associated with mirror properties, self-other processing and reward. In this review, we outline three potential models linking these regions with cognitive consequences of being mimicked. The models suggest that positive downstream consequences of mimicry may depend upon self-other overlap, detection of contingency or low prediction error. Finally, we highlight limitations with traditional research designs and suggest alternative methods for achieving highly ecological validity and experimental control. We also highlight unanswered questions which may guide future research.

Keywords: mimicry, imitation, nonverbal behaviour, neurocognitive models

It is often said that imitation is the sincerest form of flattery, and copying what other people do is a central feature of human social interaction (Frith & Frith, 2012; Hamilton, 2014; Meltzoff, 2010; Over & Carpenter, 2013). One way we copy others is through unconscious behavioural mimicry, also described as ‘behaviour matching’ (Bernieri & Rosenthal, 1991; Chartrand & Bargh, 1999) or the ‘chameleon effect’ (Chartrand & Bargh, 1999). This kind of mimicry occurs when one person unintentionally and effortlessly copies another person’s posture or body movements without either one being aware (Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009). Mimicry may extend to the contagion of facial expressions (Bavelas, Black, Lemery, & Mullett, 1986, 1987; Dimberg, Thunberg, & Elmehed, 2000; Hsee, Hatfield, Carlson, & Chemtob, 1990), moods (Hsee et al., 1990; Neumann & Strack, 2000) and speech (Giles & Powesland, 1975; Neumann & Strack, 2000).

As well as mimicry, there are many other ways we coordinate our behaviour with other people during social interactions (Table 1). The umbrella term ‘interpersonal coordination’ covers a range of coordinated actions between two people, which can be linked in both space and time. Actions occurring at the same time are described as entrained or synchronous; this includes perfect synchrony where actions are matched in form and timing, as well as general synchrony where different actions are coordinated in time (see Table 1, column 1). Actions that occur after a delay but which are contingent on the other are termed imitation or mimicry if the form is the same, and complementary if the form is different (see column 2). There is a distinction between imitation, which is deliberate and goal-directed, and mimicry, which is unconscious and spontaneous. In this paper we will focus specifically on mimicry. For the main part we will limit our review to mimicry of postures and body movements, and we will not include literature on facial, emotional or vocal mimicry. We will also concentrate on adult mimicry rather than developmental literature. At the end, we will

return to consider how future research may situate mimicry within a wider framework of interpersonal coordination.

Table 1 about here.

Whilst partners in real life social interactions may mimic one another reciprocally, in research we typically label one person as the mimicker and one person as the mimickee. With the spotlight predominantly on the mimicker, recent research has built up a large body of evidence about the social and cognitive processes involved in mimicking another person. Data from many sources shows that people tend to spontaneously copy each other (Heyes, 2011). Production of mimicry is modulated by a number of social cues, including motivation to affiliate (Chartrand, Maddux, & Lakin, 2005; Lakin, Jefferis, Cheng, & Chartrand, 2003), in-group membership (Bourgeois & Hess, 2008; Yabar, Johnston, Miles, & Peace, 2006), eye contact (Wang, Newport, & Hamilton, 2011) and attractiveness (Karremans & Verwijmeren, 2008; Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2008; van Leeuwen, Veling, van Baaren, & Dijksterhuis, 2009). Priming can modulate the level of mimicry in an interaction, with more mimicry following affiliation, fairness or prosocial primes (Cook & Bird, 2011; Hofman, Bos, Schutter, & Honk, 2012; Lakin & Chartrand, 2003). However, these effects are reliably altered by the self-relatedness of the primes (Wang & Hamilton, 2013). Neurally, we know that mimicking another person's action engages inferior parietal cortex and premotor cortex (Grèzes & Decety, 2001; Iacoboni et al., 1999; Molenberghs, Cunnington, & Mattingley, 2009), commonly referred to as the mirror neuron system. These areas are subject to top-down control from prefrontal cortex (Brass, Ruby, & Spengler, 2009; Spengler, Brass, Kühn, & Schütz-Bosbach, 2010; Spengler, von Cramon, & Brass, 2010; Wang & Hamilton, 2012). The relationship between mirror systems and top-down control has been described in terms of the STORM model (Wang & Hamilton, 2012), and several other detailed models of mimicry and imitation have also been developed (Brass, Ruby, & Spengler, 2009; Cross,

Torrissi, Reynolds Losin, & Iacoboni, 2013; Stephanie Spengler, von Cramon, & Brass, 2009) From a theoretical point of view, mimicry has been described as a ‘social glue’ (Dijksterhuis, 2005; Lakin et al., 2003), helping us to bond with members of our social groups by creating smooth, harmonious social interactions (Lakin et al., 2003).

In contrast to this detailed evidence about the production of mimicry, we know less about how mimicees perceive and respond to being mimicked. It is widely believed that there is a bidirectional link between mimicry and affiliation, such that being mimicked should lead to more liking (Chartrand et al., 2005; Chartrand & van Baaren, 2009; Lakin & Chartrand, 2003). However, the cognitive processes underlying this link are not yet clear. Therefore in the current paper we aim to critically review the literature on mimicees’ social and cognitive reactions to being mimicked and outline possible theoretical models that could direct future research. In the first section of this review we re-examine whether being mimicked leads to positive responses (e.g. liking and trust) and discuss different modulators of the positive effects of mimicry. In the second section, we will consider neuroimaging studies in which participants were mimicked, imitated or acted in synchrony, in order to inform possible neurocognitive models which can account for the behavioural data reviewed in the first section. Our aim here is to present speculative accounts which develop different theoretical ideas in the literature, so as to stimulate future discussion and research into the neurocognitive mechanisms of mimicry interactions. In the third section, we consider methodological challenges in studies which have been conducted so far, and suggest future directions which may overcome these challenges. Finally, we turn to unanswered questions and a broader scope for mimicry research.

1. How do people respond to being mimicked?

1.1 Positive Responses to Mimicry

1.1.1 Affiliation & trust. There is a strong consensus that people respond positively to being mimicked. Initially, researchers observed that mimicry during clinical therapy sessions (Cappella & Planalp, 1981; Schefflen, 1964, 1972) and classroom interactions (Bernieri, 1988; Bernieri & Rosenthal, 1991; LaFrance, 1979; LaFrance & Broadbent, 1976) was correlated with reported affiliation, empathy and rapport. Several early experiments manipulated posture congruency and found that confederates who mirrored the posture of participants were evaluated as more similar (Dabbs Jr., 1969; Navarre, 1982), empathic (Maurer & Tindall, 1983) and sociable (Navarre, 1982). Then, in a seminal study, Chartrand & Bargh (1999, Experiment 2) trained confederates to manipulate the level of mimicry in an interaction. Each participant spent fifteen minutes with a confederate, taking turns to describe various photographs. In the mimicry condition, the confederate mirrored participants' posture, gestures and mannerisms; in the control condition, the confederate maintained a neutral posture. At the end of the session, participants who were mimicked rated the confederate as significantly more likeable and the overall interaction as significantly more smooth than participants in the control condition. Following this study, the confederate paradigm became a popular method for studying mimicry effects (Stel, Rispens, Leliveld, & Lokhorst, 2011; Van Baaren & Chartrand, 2005; van Baaren, Holland, Kawakami, & van Knippenberg, 2004), and researchers have worked under the assumption that one of the fundamental effects of mimicry is to increase liking towards the mimicker (e.g. Chartrand & Lakin, 2013; Lakin et al., 2003; Stel et al., 2010).

However, this basic link from mimicry to liking has not been replicated consistently. Ten studies which measured liking in response to mimicry are summarised in Table 2. Four experiments have replicated Chartrand & Bargh's (1999) result using the confederate

paradigm (Kouzakova, Karremans, van Baaren, & van Knippenberg, 2010; Kouzakova, van Baaren, & van Knippenberg, 2010; Stel et al., 2011, Study 1). One experiment replicated this finding within ‘prosocial’ but not ‘proself’ participants (Stel et al., 2011, Study 2). Two experiments using the confederate paradigm failed to replicate the mimicry-liking link, despite reporting significant effects of mimicry on other measures (Drury & van Swol, 2005; van Swol, 2003). Similar results were reported by a much earlier experiment on posture congruency (Dabbs Jr., 1969). Bailenson and Yee (2005) found positive effects using a virtual mimicry paradigm: in their experiment, participants wore a head mounted display (HMD) which let them see a virtual character in an immersive virtual environment. The HMD tracked participants’ head movements and the virtual character either mimicked their movement or made head movements recorded from a previous participant, while delivering a persuasive speech. Participants who were mimicked rated the character as more effective on a composite scale which included likability (Bailenson & Yee, 2005), although the weighting of likeability was unclear. Another virtual mimicry study found a positive effect on liking for one out of two virtual characters that mimicked participants in the same way (Verberne, Ham, Ponnada, & Midden, 2013). Finally, Maddux, Mullen and Galinsky (2008, Study 2) instructed participants to either mimic or not mimic their partner during a business negotiation task, and found that mimicry did not lead the partners to rate more liking for each other. Overall, only 5 of 10 studies found a direct mimicry-liking link, and our list does not include studies which have not been published due to negative results. Even the studies which have found positive results report small effect sizes (eta squared close to 0.1)

Table 2 about here.

The effects of mimicry on trust towards the mimicker appear to be similarly inconsistent. In the same business negotiation task, Maddux et al. (2008, Study 2) found that the amount of time participants self-reported mimicking their partner was significantly

correlated with the partner's rating of trust towards the mimicker, and the partner's trust mediated a positive effect of mimicry on the likelihood of negotiating a successful deal. In line with these findings, Verberne et al. (2013) found people rated more trust towards a virtual character that mimicked them, and mimicry also increased participants' willingness to trust the virtual character in a decision-making task. However, they could not replicate these results with a second character and a different behavioural measure. Thus, the effects of mimicry on implicit trust behaviour may be mimicker- and task-dependent (Hasler, Hirschberger, Shani-Sherman, & Friedman, 2014). Similar to the studies measuring liking, these results suggest that being mimicked may not reliably increase trust in the mimicker across all contexts.

1.1.2 Prosocial and self-related changes. A reliable positive consequence of mimicry is an increase in prosocial behaviour. Following mimicry, participants are not only more likely to agree with an explicit request for help (Guéguen, Martin, & Meineri, 2011), they are also more spontaneously helpful: van Baaren et al. (2004, experiment 1) found that people who were mimicked by an experimenter while taking turns to describe advertisements were more likely to pick up some pens she dropped after the end of the task. In a follow-up experiment, people who were mimicked were also more likely to help an unrelated experimenter (van Baaren et al., 2004). Similar responses were recently demonstrated in infants aged 18 months using an adaptation of the same paradigm (Carpenter, Uebel, & Tomasello, 2013). In other contexts, being mimicked made participants more willing to help an unknown researcher by filling out a tedious questionnaire (Ashton-James, van Baaren, Chartrand, Decety, & Karremans, 2007) and made people passing along a street more compliant with a stranger's request for help (Fischer-Lokou, Martin, Guéguen, & Lamy, 2011). As well as helping, mimicry leads people to donate more money to charity, regardless of whether the charity is connected to the mimicker (van Baaren et al., 2004). People may

even be more inclined to vote for prosocial left-wing political parties following mimicry (Stel & Harinck, 2011). Taken together, these findings suggest that mimicry elicits prosocial responses which extend beyond the mimicry interaction (Van Baaren & Chartrand, 2005; van Baaren et al., 2004).

Mimicry also appears to influence or affect the self-construal of the person being mimicked. When completing a ‘twenty statements’ measure of self-construal (Kuhn & McPartland, 1954), in which people may define themselves by relationships with other people (interdependently) or without reference to others (independently), people reliably provide more interdependent statements following mimicry (Redeker, Stel, & Mastop, 2011; Stel & Harinck, 2011; Stel et al., 2011). Participants who were mimicked also felt closer to others when completing an ‘inclusion of other in the self’ (IOS) scale (Aron, Aron, & Smollan, 1992), which depicts increasingly overlapping circles representing self and other (Ashton-James et al., 2007, Experiment 2). As well as feeling closer to others, participants who have been mimicked are more likely to connect objects with their surrounding context and see similarities between photographs which are not systematically related (van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009). They also show less divergent thinking and more convergent thinking, which can facilitate collaboration (Ashton-James & Chartrand, 2009). Together, these studies suggest that being mimicked leads to both an interdependent self-construal and prosocial behaviour. Notably, these effects have been demonstrated together (Ashton-James et al., 2007; Catmur & Heyes, 2013; Stel & Harinck, 2011) and Ashton-James et al. (2007, Study 4) found that self-construal mediated the effect of mimicry on prosocial behaviour. We will return to this causal link in the next section.

1.1.3 Changing opinions. Being mimicked can change people’s opinions and behaviour in a number of ways. Mimicry increases perceived smoothness in an interaction(Chartrand & Bargh, 1999). For example, people were more likely to disclose

intimate information (Guéguen, Martin, Meineri, & Simon, 2013) or give honest answers (Guéguen, 2013) to a confederate who mimicked them. Mimickers are also rated as being more persuasive than non-mimickers (Bailenson & Yee, 2005; Drury & van Swol, 2005; van Swol, 2003), and may sometimes be more successful in swaying people to agree with their opinion (Bailenson & Yee, 2005, but see van Swol, 2003) or to consume and purchase goods (Herrmann, Rossberg, Huber, Landwehr, & Henkel, 2011; Jacob, Guéguen, Martin, & Boulbry, 2011; Tanner, Ferraro, Chartrand, Bettman, & Baaren, 2008). Furthermore, mimicry can improve negotiation outcomes (Maddux et al., 2008): participants who negotiated for around 30 minutes had better personal and joint outcomes when one member of the dyad was instructed to mimic (Maddux et al., 2008). These outcomes suggest that mimicry could indeed be a beneficial social strategy for inducing compliance (Lakin et al., 2003). However, increasing conformity of opinions is not always positive. Mimicry can make participants conform to stereotypes consistent with group stereotypes even when those are negative towards the participant and the participant does not endorse them (Leander, Chartrand, & Wood, 2011). Together, these studies suggest that being mimicked may make participants more conformist or likely to agree, with both the good and bad consequences that can bring.

1.2 Factors Modulating Positive Responses to Mimicry

1.2.1 Mimicker factors. A large number of factors can alter the general picture that mimicry has positive and prosocial effects. This is particularly clear in situations where people interact with a member of their social outgroup. People typically produce less mimicry towards others who they initially dislike (Stel et al., 2010), outgroup members (Bourgeois & Hess, 2008; Yabar, Johnston, Miles, & Peace, 2006), and others from a different race (Johnston, 2002). Being mimicked by someone from an outgroup does not seem to have the same prosocial consequences as ingroup mimicry. For example, following mimicry from an ingroup (White) or outgroup (Black) confederates, Dalton et al. (2010, Experiment 2) gave

participants a Stroop task as a measure of cognitive resource depletion. The results showed a significant interaction between mimicry and race: participants who were mimicked by a confederate of the same race showed less resource depletion than people who were not mimicked; on the other hand, participants who were mimicked by someone of a different race showed more resource depletion than people who were not mimicked (Dalton et al., 2010). Mimicry by an outgroup member also leads participants to report a room as colder than mimicry from an ingroup member (Leander, Chartrand, & Bargh, 2012, Experiment 3).

Similar effects are found when social status and affiliation is manipulated. Dalton et al. (2010) manipulated status by assigning participants to the role of leader or follower and a confederate to the other role. Participants who were mimicked by a leader showed more resource depletion in a later Stroop task, compared to those mimicked by a follower (Dalton et al., 2010, Experiment 3). Participants who were mimicked by a confederate expressing affiliation showed positive consequences of mimicry, whereas those mimicked by a task-focused confederate did not (Leander et al. 2012, Experiment 1). A plausible explanation for all these effects is that mimicry only has positive consequences in contexts where it is expected. If being mimicked is unexpected, because a partner is an outgroup member or of higher status or not interested in affiliating, then participants do not respond in the same way to being mimicked.

1.2.2 Mimickee factors. The consequences of mimicry may also depend critically on the personality or other features of the participant being mimicked. In particular, people who are highly ‘proself’ rather than ‘prosocial’ may not respond positively to being mimicked. Stel et al. (2011) defined participants as prosocial if they consistently chose to benefit another player in a game, and proself if they played the game competitively or for individual gain. The prosocial participants reacted positively to being mimicked and indicated more liking towards a mimicker than a non-mimicker; however, this effect was absent in proself

participants (Stel et al., 2011). Similarly, although mimicry usually causes people to feel more interdependent, people who naturally have a strong independent self-construal could find it uncomfortable to be mimicked. Highly independent people underestimated the room temperature as a result of mimicry; in contrast, highly interdependent people underestimated temperature when they were not mimicked (Leander et al., 2012, Experiment 2). Individual differences in self-construal can reflect differences in cultural background (Markus & Kitayama, 1991), which may modulate responses to mimicry in a similar way. Sanchez-Burks et al. (2009) showed that US Latino participants, whose culture emphasises social harmony, felt anxious when interviewed by a confederate that did not mimic them, whereas this was not observed in US Anglos. Overall, a variety of findings indicate that people who highly value personal gain or feel independent from others may not show the expected positive reactions to being mimicked.

Social anxiety may also prevent some individuals from responding positively to mimicry. People with high social anxiety tend to focus on themselves and feel awkward during conversations (Heerey & Kring, 2007). Therefore it is not surprising that women with high social anxiety mimic others less than non-socially anxious women (Vrijnsen, Lange, Becker, & Rinck, 2010). However, Vrijnsen Lange, Dotsch, Wigboldus, & Rinck (2010) also found that women with high social anxiety do not respond positively when they are mimicked by someone else. In their study, women listened to two virtual characters give an opinionated speech; one mimicked participants' head movements and the other did not mimic. Socially anxious women evaluated both character as similarly likable, friendly and convincing, whereas non-socially anxious women evaluated the mimicking character more highly (Vrijnsen, Lange, Dotsch, et al., 2010). This suggests that being mimicked may not have prosocial effects in individuals who focus on themselves due to high social anxiety.

Finally, the prosocial effects of mimicry are expected to break down when people become aware they are being mimicked (Ashton-James et al., 2007; Chartrand & Bargh, 1999; Dalton et al., 2010; Guéguen et al., 2013). However, very few studies have directly addressed this expectation, as it is common practice to exclude participants who detected mimicry manipulations from analyses (e.g. Bailenson & Yee, 2005; Cheng & Chartrand, 2003; Drury & van Swol, 2005; van Swol, 2003). Bailenson et al. (2008, Experiment 2) explicitly tested how people respond when they detect they are being mimicked. A virtual character mimicked participants' head movements while delivering a persuasive speech in an immersive virtual environment. Eighty per cent of participants detected they were being mimicked; these participants rated the character as significantly less warm and trustworthy compared participants who did not detect mimicry (Bailenson et al., 2008), suggesting that people may only respond positively to mimicry when they are unaware it is happening.

1.3 Summary

As previous reviews have described (Chartrand & Dalton, 2009; Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009; van Baaren, Janssen, et al., 2009), there are a variety of ways in which people respond positively to mimicry. Mimicry can change people's perception of the mimicker, including judgements of likeability and trust, although these effects are not very reliable. Mimicry can change a participant's self-construal, leading an increase in prosocial behaviour, and may also increase agreement and conformist behaviour. These effects are modulated by characteristics of both the mimicker and mimickee. If characteristics of the mimicker make mimicry seem unlikely, including outgroup membership or high status, then participants do not respond positively to mimicry. Participants who are naturally independent or socially anxious also report less positive effects of mimicry. In the following section, we review neural systems which respond to being mimicked and consider possible neurocognitive models which could help us understand these effects.

2. Neurocognitive Mechanisms for Responding to Mimicry

2.1 Neural Correlates of Being Mimicked

There is little data on the neural correlates of being mimicked, owing to the difficulty of studying this spontaneous social interaction under controlled conditions (Guionnet et al., 2012). Only one study has measured a mimickee's neural response to mimicry of their postures and body movements (Hogeveen, Chartrand, & Obhi, 2014). However, several other research groups have measured neural activation in response to closely related experiences, including being overtly imitated by a live experimenter or a video stimulus (Brass et al., 2009; Decety, Chaminade, Grèzes, & Meltzoff, 2002; Guionnet et al., 2012), passively observing a mimicry interaction from the perspective of the mimickee (Kühn et al., 2010), and interactional synchrony driven by another person (Cacioppo et al., 2014; Kokal, Engel, Kirschner, & Keysers, 2011). Here we consider the available data from these different paradigms in order to infer possible neural systems involved in responding to mimicry. The studies (summarised in Table 3) highlight three systems involved in responding to mimicry: (1) a perception-action matching system which recognises when we are being mimicked, (2) a self-other system which relates actions made by self and other, and (3) a reward system associated with positive affect and prosocial behaviour (Figure 1).

Figure 1 about here.

2.1.1 Perception-action matching. There is extensive evidence that the production of mimicry relies on the mirror system regions of inferior parietal and inferior frontal cortex (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004). These are robustly activated when people produce actions, observe actions and imitate actions (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs, Cunnington, & Mattingley, 2009). These same regions are also likely to have a role in detecting when someone else is mimicking, because they have the

capacity to match observed to performed actions. One study tested this using EEG recordings of the mu-rhythm, a possible marker of MNS function. Hogeveen et al. (2014) took EEG recordings before and after participants completed a rating task. The task involved one of three conditions: social interaction with a mimicking confederate, social interaction with an anti-mimicking confederate, or interaction with a computer. During EEG recording, participants observed video actions. Their mu-rhythm suppression, which is thought to reflect activation of the sensorimotor cortex, was measured as an indirect index of MNS activity. The results showed enhanced mu-suppression from pre- to post-test in the mimicry condition. The same increase was not found in the anti-mimicry condition, and the increase was significant relative to the computer condition. These findings suggest that being mimicked during naturalistic social interaction leads to an increase in MNS activity which can be detected during subsequent action observation.

Two neuroimaging studies provide evidence that being imitated leads to activation in the left inferior parietal cortex, a classic region of the MNS (Molenberghs et al., 2009; Rizzolatti & Craighero, 2004). Decety et al. (2002) used PET to measure participants' brain activity in response to deliberately imitating or being imitated by an experimenter. The experimenter and participant each had a set of three small objects to manipulate with their right hand and they could see each other's hands via live video links. In this paradigm, participants knew in advance whether they were about to be imitated or not in each block of the experiment. There was an increase in activity in the left inferior parietal cortex when participants were imitated by the experimenter as well as when they did the imitating. Similar activity was found in recent fMRI study of participants who experienced another person not in their view (actually a computer algorithm) synchronising with them on a computer screen while the participant simply tapped a button (Cacioppo et al., 2014). Compared to experiencing asynchrony, while participants experienced synchrony they showed greater

activity in the left inferior parietal cortex. Therefore, converging evidence from mimicry, imitation and synchrony paradigms suggests the MNS is involved in the unconscious recognition of mimicry through perception-action matching.

2.1.2 Relation between self and other actions. Being mimicked also appears to activate several regions associated with self-other processing. Decety et al. (2002) found that being imitated was associated with stronger activation in the right inferior parietal cortex, compared to imitating someone. This region is thought to have a role in self-other discrimination and sensing agency (Decety & Sommerville, 2003; Farrer & Frith, 2002; Ruby & Decety, 2001; Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006). Consistent with this finding, Brass et al. (2009) found significant activation in the TPJ in response to being imitated. In their fMRI study, participants made index or middle finger movements that were congruent or incongruent with a stimulus movement, and either saw the stimulus movement before or after they responded. Similar levels of TPJ activity were observed when the participant was imitated and when they experienced an incongruent stimulus. This pattern of results is consistent with the interpretation that TPJ responds when observed movements are delayed or dissimilar performed movements, suggesting this region is involved in distinguishing between self and other actions or perspectives (Brass et al., 2009; Jean Decety & Sommerville, 2003; Ruby & Decety, 2001; S. Spengler, von Cramon, & Brass, 2010).

However, other results suggest that being mimicked is associated with increased self-other overlap in frontal regions. Kuhn et al. (2010) set out to investigate the neural correlates of positive responses to mimicry. Specifically, participants in an fMRI scanner passively observed videos of social interactions where they took the first-person perspective of an actor being mimicked or anti-mimicked. Compared to anti-mimicry, mimicry led to increased activity in the mOFC/vmPFC, which correlated with ratings of interpersonal closeness. Therefore, being mimicked may be associated with processes of self-other overlap in

mOFC/vmPFC in addition to processes of self-other distinction in TPJ and inferior parietal cortex.

2.1.3 Positive responses to mimicry. Neuroimaging data also highlight a system of reward activation in response to being mimicked. In the study described above, Kuhn et al. (2010) also demonstrated activation in brain areas associated with emotion and reward processing. The mimicry condition was associated with increased functional connectivity between vmPFC and the striatum and mid-posterior insula, regions which are related to positive affective states and emotional salience (Craig, 2005; Kühn et al., 2010; Uddin, 2015). In a different paradigm, Guionnet et al. (2012) used live video links to study neural activity while being imitated in an fMRI scanner. Participants either moved their hands and were imitated by an experimenter, or imitated the experimenter's hand movements. Consistent with the functional connectivity reported by Kuhn et al. (2010), there was greater activation in the left anterior insula when participants were imitated. These findings indicate that a reward network involving the striatum and insula may be activated in connection to vmPFC in response to being mimicked.

Further evidence for the same reward system comes from an fMRI study of synchronous behaviour. Kokal et al. (2011) examined activity in the caudate during a drumming task in which participants experienced a partner drumming in synchrony or asynchrony with them. They found that that ease of drumming was associated with activation in the caudate, a region also active in processing monetary reward. Importantly, caudate activation while drumming in synchrony predicted prosocial behaviour towards the drumming partner at the end of the experiment. These findings provide evidence for a neural link from synchrony-related reward processing to downstream prosocial behaviour, which has previously been found to follow synchronised behaviour and mimicry (P. Valdesolo & DeSteno, 2011; van Baaren et al., 2004; Wiltermuth & Heath, 2009).

2.2 Neurocognitive Models of Being Mimicked

From these initial neuroimaging results, it seems that being mimicked may activate three neural systems, one which detects mimicry (MNS), one which relates self and other actions (TPJ and vmPFC), and one which reflects the positive consequences of mimicry (striatum and insula). However, there are very few data points here which makes it hard to develop a cognitive model of how these systems might operate together when someone is being mimicked. To advance the field, we can also draw on our extensive knowledge of brain systems engaged in relevant cognitive processes, in particular perception-action matching, social reward processing and perspective-taking. Numerous studies have shown that imitating other people's actions and observing action engages the MNS (Caspers et al., 2010; Molenberghs et al., 2009, 2009). There is also a large body of literature showing that socially rewarding activities engage the insula, ventral striatum and OFC (e.g. Aharon et al., 2001; Bhanji & Delgado, 2014; Fliessbach et al., 2007; Izuma, Saito, & Sadato, 2008; O'Doherty et al., 2003; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). In addition, several lines of evidence suggest that perspective-taking and other forms of self-other processing engage mPFC and TPJ (Brass, Derrfuss, & von Cramon, 2005; David et al., 2006; Denny, Kober, Wager, & Ochsner, 2012; Heatherton et al., 2006; Ruby & Decety, 2001). Drawing on this knowledge in conjunction with the specific studies of being mimicked (reviewed above), we can then begin to propose cognitive models which link together these systems and suggest how they may relate to the behavioural effects of being mimicked. Here we will outline three possible models which draw from existing theoretical ideas in the literature and develop them in relation to the neuroscientific evidence reviewed above. We note that all three models are highly speculative, and hope that they will inspire future work to test and distinguish between them. We will also consider how well each model can account for the current data on behavioural responses to being mimicked.

2.2.1 Self-Other Overlap model. One possible model linking neural and behavioural responses to being mimicked could depend upon self-other processing. During mimicry, the boundary between self and other is thought to become blurred (Georgieff & Jeannerod, 1998), and Ashton-James et al. (2007) have proposed that an increase in self-other overlap mediates the prosocial consequences of being mimicked. The Self-Other Overlap model builds on this cognitive pathway by speculating that when perception-action matching occurs in the MNS, regions involved in self-other processing are activated. In turn, frontal regions associated with interpersonal closeness may activate a reward system involving the insula and caudate, which may lead to an increase in prosocial behaviour (Kokal et al., 2011). Other positive responses to mimicry may also result from this cognitive pathway, although only prosocial behaviour has been previously tested (Ashton-James et al., 2007)

Importantly, the Self-Other Overlap model assumes that being mimicked leads to a general tendency to see oneself as closer to others (Ashton-James et al., 2007), despite neural activation in TPJ and inferior parietal cortex associated with self-other distinction (Brass et al., 2009; J. Decety et al., 2002). Several lines of research suggest that the ability to distinguish self- and other-perspectives is essential for taking another's perspective (Galinsky, Ku, & Wang, 2005; Lamm, Batson, & Decety, 2007), which may be an important process in empathy (Bird & Viding, 2014; Jean Decety & Jackson, 2006) and prosocial cooperation (Galinsky et al., 2005; Maddux et al., 2008). Therefore, this model assumes that mimicry ultimately leads people to see others as more 'like me' (Meltzoff, 2007a, 2007b) and behave more prosocially as a result of this self-other overlap.

The Self-Other Overlap model can account for many of the positive responses to mimicry reviewed earlier. In particular, several research groups demonstrated that being mimicked makes people behave prosocially towards others in general, and not just the person mimicking (Ashton-James et al., 2007; Carpenter et al., 2013; J. Fischer-Lokou et al., 2011;

Stel & Harinck, 2011; van Baaren et al., 2004). In fact, no studies have reported social effects of being mimicked which failed to extend to other people beyond the mimicker. Furthermore, being mimicked induces cognitive changes in feelings of interdependence (Redeker et al., 2011; Stel & Harinck, 2011; Stel et al., 2011), social distance (Ashton-James et al., 2007) and convergent thinking (Ashton-James & Chartrand, 2009). These findings are consistent with the suggestion that being mimicked primarily increases self-other overlap, and other consequences are secondary. If people tend to rate mimickers as more likeable, trustworthy or persuasive due to a general prosocial effect rather than a change in their perceptions of the mimicker, this could also explain why mimicry appears to have less robust effects on these ratings compared to prosocial behaviour.

However, Hogeveen et al. (2014) found mimicry did not lead to increased self-other overlap using the IOS scale, which is inconsistent with the model's predictions. The Overlap model also does not explain why the positive effects of mimicry are modulated by characteristics of the mimicker. If being mimicked primarily increases self-other overlap, it is unclear why participants do not respond positively to mimicry from an outgroup member (Dalton et al., 2010; Leander et al., 2012), higher status person (Dalton et al., 2010) or task-focused individual (Leander et al., 2012). Arguably, increased self-other overlap should have especially notable effects in these interactions, because the initial level of overlap may be lowered.

2.2.2 Contingency model. Whereas the first model proposed that perception-action matching is linked to reward via self-other processing, the Contingency model assumes that detecting contingency between our own actions and the world is intrinsically rewarding and motivating. Under this model, complementary and imitative actions would all be processed in the same way and be equally rewarding. From infancy, the ability to detect contingent caregiver behaviour is found to increase positive affect, self-efficacy and social motivation

towards the caregiver (Dunham, Dunham, Hurshman, & Alexander, 1989; Millar, 1988; Watson & Ramey, 1972). The Contingency model therefore proposes that being mimicked leads to positive responses due to the contingency of the mimicker's actions on the mimicked's. This view is supported by a recent study showing that people responded positively to contingent movements regardless of how similar the movements were to their own (Catmur & Heyes, 2013), suggesting that positive responses to mimicry may be attributed to contingency and not behaviour-matching. The MNS may be responsible for detecting this contingency. Several studies provide evidence that mirror associations in the MNS are learned through contingent experience, by demonstrating the MNS can form similar associations between dissimilar actions through repeated contingent experiences (Catmur et al., 2008; Catmur, Walsh, & Heyes, 2007; Heyes, 2001). Therefore, when the MNS is active in responding to mimicry it may actually reflect the detection of contingency.

The contingency model would predict that positive affective and social consequences of detecting contingency can be attributed to activation of the neural reward system. However, this system may be tuned to an expected *level* of contingency. Infant studies show that contingent behaviour from a stranger only elicits positive responses when the degree of contingency is similar to their caregiver's behaviour (Bigelow, 1998, 2001). Research in robotics also highlights the importance of 'appropriate' contingency levels in creating realistic social entities (Yamaoka, Kanda, Ishiguro, & Hagita, 2006, 2007). Therefore, the Contingency model would also predict that reward is not a fixed response to being mimicked.

In support of the Contingency model, being in synchrony has similar positive effects to being mimicked. In particular, synchronised movement leads to increased liking (Hove & Risen, 2009; Lynden K. Miles, Nind, & Macrae, 2009) and prosocial behaviour (Reddish, Fischer, & Bulbulia, 2013; Piercarlo Valdesolo, Ouyang, & DeSteno, 2010; Wiltermuth & Heath, 2009). Synchrony and mimicry also appear to activate similar reward regions in the

brain (Cacioppo et al., 2014; Kokal et al., 2011). Since synchronised movements are characterised by temporal contingency rather than similarity (Catmur & Heyes, 2013), this suggests that contingency may explain these effects of mimicry. Decreasing the time lag in mimicking is also thought to elicit stronger responses and make mimicry easier to detect (Bailenson, Beall, Loomis, Blascovich, & Turk, 2004). The Contingency model is also consistent with the breakdown of positive responses to mimicry in contexts and individuals where a lower level of mimicry is typical (Dalton et al., 2010; Leander et al., 2012).

However, whether mere contingency is ‘enough’ or whether the similarity of actions has additional importance is a matter of debate. The Contingency model we have outlined is directly challenged by studies comparing merely contingent behaviour to mimicry: in both infants (Agnetta & Rochat 2004) and adults (Hogeveen et al., 2014; Kulesza, Szypowska, Jarman, & Dolinski, 2014), mimicry elicits more positive responses than contingent behaviour or anti-mimicry. People also show a preference for movements that involve the same effector even when there is no temporal contingency (Sparenberg, Topolinski, Springer, & Prinz, 2012), which suggests that similarity of movement may still account for some of the positive effects of being mimicked.

2.2.3 Similarity model. Like the Contingency model, the Similarity model proposes a direct pathway from perception-action matching to reward activation, and makes the claim that the most predictable response from the other person is the one with the highest reward value. In this context, the similarity model assumes that an imitative action is more rewarding than a non-imitative one because the kinematic similarity of imitation makes it easier to predict the imitative pattern of action. This means that imitative actions would be more rewarding than complementary actions. Note that overlearning complementary actions (e.g. the grasp patterns involved in handing a mug to another person) might also be highly predictable and thus rewarding.

There is increasing evidence that the brain is good at prediction in both perception and action (Brown & Brüne, 2012; Bubic, von Cramon, & Schubotz, 2010; Clark, 2013). In line with this evidence, the Similarity model assumes the brain is a predictive system which aims to anticipate future sensory inputs (Friston, Mattout, & Kilner, 2011; Kilner, Friston, & Frith, 2007), and which finds predictable inputs rewarding. Within this framework, the MNS is part of a generative model that tries to predict incoming sensory input (Kilner, 2011). Using knowledge of a participant's own action and of the social context, the MNS can generate predictions about what the other person will do and can compare those to the other's actual action. If the other person mimics the participant, the visual input is predictable because it is similar to the participant's own action, leading to a low prediction error signal. However, if the other person does not mimic but instead performs some other contingent action, the visual input is less predictable and the error signal is higher. This means that interacting with someone who mimics leads to less prediction error and more activation of reward-related brain networks, which could induce a positive or prosocial mood.

Like the Contingency model, the Similarity model could also generalise to take into account contextual expectations of mimicry. It has previously been suggested that not being imitated is generally unexpected, and therefore experienced negatively (van Baaren, Decety, Dijksterhuis, van der Leij, & van Leeuwen, 2009). If a participant is in a context where mimicry is likely (e.g. interacting with an in-group member), then their MNS will generate a mimicry prediction and when this matches their visual input, prediction error is low and reward is high. However, if a participant is in a context where mimicry is not likely (e.g. interacting with an outgroup member), then their MNS will predict other actions which are not similar to their own. If the interaction partner does mimic, the visual input concerning their actions will not match the predicted visual input, leading to a high prediction error and

low reward. Note that this generalisation would require additional contextual information to modulate what the MNS predicts.

By taking mimicry context into account, the Similarity model is able to explain both positive consequences of being mimicked and the breakdown of these positive consequences in certain contexts. Many of the positive effects of mimicry, such as affiliation (Chartrand & Bargh, 1999; Stel & Vonk, 2010), persuasion (Drury & van Swol, 2005; van Swol, 2003) and perceived smoothness (Chartrand & Bargh, 1999) could be direct consequences of reward activation during social interaction. The suggestion that these positive responses depend on the expectation of being mimicked is also consistent with studies showing that mimicry from an outgroup member, high status person or disaffiliative person challenges our expectations, leading to cognitive resource depletion (Dalton et al., 2010) and negative responses (Leander et al., 2012). The Similarity model is also consistent with data suggesting that individual differences in self-construal mediate whether people respond positively to being mimicked. Considering that self-construal is closely tied to cultural norms (Markus & Kitayama, 1991; Sanchez-Burks et al., 2009), people with strongly independent self-construals may expect to be mimicked less often than people who feel strongly interdependent (Sanchez-Burks et al., 2009; Stel et al., 2011). Thus, people with independent self-construals may not respond positively to mimicry because they do not predict mimicry will occur.

However, this model is less clear in explaining the robust link between mimicry and prosocial behaviour. It is unclear why a low prediction error and subsequent reward activation should lead to prosocial responses such as helping other people, and why prosocial behaviour should extend beyond the person mimicking (Van Baaren & Chartrand, 2005; van Baaren et al., 2004). Others have suggested that positive affect may be associated with creative and prosocial cognitive styles (Ashton-James & Chartrand, 2009), but there is no clear evidence for a pathway from reward activation to positive affect to generalised

prosocial behaviour. Given that increased prosocial behaviour appears to be one of the most consistent effects of being mimicked, this is a significant limitation of the Similarity model.

2.3 Summary

The available neuroimaging and EEG data from mimicry, imitation and synchrony tasks suggested that being mimicked may activate mirror neuron systems, brain regions for self-other processing and reward-related systems. We have outlined three speculative models which link these neural systems to possible cognitive processes that follow being mimicked. The Self-Other Overlap model suggests that recognising a perception-action match in the MNS may lead to neural reward via self-other processing; in contrast, the Contingency model and Similarity models propose a direct link between perception-action matching and reward activation (Figure 1). The Contingency model argues that this link depends purely on the temporal contingency of the mimicker's actions on the mimickee's and that the kinematic form of their actions is not relevant. In contrast, the Similarity model suggests that kinematic similarity between mimicker and mimickee movements increases the predictability of the mimicker's behaviour, which reduces prediction error and increases reward.

Each model is able to predict some of the reported outcomes of being mimicked. However, none of them fully explain the range of findings reviewed in the first section. This suggests the effects of being mimicked could be explained by a combination of the models above or other models we have not outlined here. We hope that the models above will provide starting points for theoretically-driven discussion and research into the processes underlying people's responses to mimicry. To develop more accurate models, it will be important to perform studies which carefully control levels of contingency and predictability, and which find better ways to measure the consequences of being mimicked.

In the next section we will review some of the methodological challenges limiting traditional paradigms for studying mimicry effects and highlight future directions which may

overcome these challenges. We will also discuss aspects of mimicry which have so far received little attention and may be relevant to future theorising about the consequences of being mimicked.

3. Methodological Challenges and Future Directions

3.1 Challenges

3.1.1 Manipulating mimicry. The first major challenge in testing the consequences of being mimicked is to achieve a well-controlled manipulation of mimicry. Since mimicry normally occurs unconsciously (Chartrand & Lakin, 2013; Chartrand, Maddux, & Lakin, 2005), it is inherently difficult to generate or eliminate. A compromise is to instruct participants or confederates to mimic in one experimental condition and refrain from mimicking in a control condition. Although this kind of instructed mimicry can reach similar levels to spontaneous mimicry (Stel, Dijk, & Olivier, 2009; Stel, van den Heuvel, & Smeets, 2008), this is not guaranteed. If untrained participants are instructed to mimic it is necessary to perform manipulation checks, such as asking the participant to report how well they followed the instruction (Maddux et al., 2008) or video recording their behaviour (Stel & Vonk, 2010). Even with trained confederates, it may be hard to achieve consistent performance (Fox et al. 2009).

It may also be hard to control extraneous variables. The instruction to mimic imposes cognitive demands which could change other aspects of the social interaction, such as emotional understanding (Stel et al., 2009). Furthermore, it is impossible for a confederate to be blind to experimental condition, and hard for them to be blind to the research hypothesis. It is also possible differences in non-mimicry behaviour from confederates between conditions could influence the experimental results, without confederate or experimenter

being aware of this. For example, postural mimicry is normally intertwined with emotional and vocal imitation (Chartrand & Lakin, 2013; Chartrand et al., 2005), and other types of coordination like synchrony (Bernieri & Rosenthal, 1991), turn-taking (Pentland, 2010; Wallbott, 1995) and eye contact (Wang, Newport, & Hamilton, 2011). Sometimes these behaviours are deliberately included in the mimicry manipulation (e.g. synchrony, Chartrand & Bargh, 1999; facial and vocal imitation, Stel et al., 2011), but researchers wishing to control for these variables must usually video their experiment and code the behaviour post hoc (e.g. Chartrand & Bargh, 1999; Drury & van Swol, 2005; Sanchez-Burks et al., 2009; van Swol, 2003).

There are also challenges associated with achieving a good control condition. In some paradigms, the control condition is defined as non-mimicry, i.e. neutral movements (e.g. Chartrand & Bargh, 1999; Kouzakova, Karremans, et al., 2010; van Baaren et al., 2004). In other paradigms, the control condition involves anti-mimicry, i.e. deliberately dissimilar movements (e.g. Ashton-James et al., 2007; Hasler, Hirschberger, Shani-Sherman, & Friedman, 2014). These conditions may have significantly different effects; for example, people bought significantly more products when they were not mimicked compared to anti-mimicked (Kulesza et al., 2014). Therefore, researchers need to consider the appropriate control condition to use.

3.1.2 Measuring mimicry effects. The second major challenge is to find valid ways of measuring how being mimicked affects a participant. Ratings of the mimicry interaction are easy to administer and widely used (e.g. Bailenson & Yee, 2005; Chartrand & Bargh, 1999; Stel et al., 2011; Stel & Vonk, 2010; Vrijnsen, Lange, Dotsch, et al., 2010). However, there are no standardised rating scales for many of the constructs of interest in mimicry research, such as liking and rapport (see Table 2). Besides subjective ratings, it is also useful to measure behavioural responses. A wide variety of behavioural measures have been used,

including Stroop task reaction times (Dalton et al., 2010), estimates of room temperature (Leander et al., 2012), the number of pens picked up (van Baaren et al., 2004), and seat choice (Ashton-James et al., 2007). These measures have the advantage of measuring participants' implicit reactions to being mimicked but are not very closely related to the mimicry itself and could be influenced by other factors. Better measures of the consequences of mimicry, both behavioural and neural measures, will be very valuable.

3.1.3 Moderators of mimicry effects. An additional challenge is to test how mimicry effects are modulated by social contexts and characteristics of the mimicker. This challenge particularly applies to confederate paradigms which manipulate mimicry within a live interaction (e.g. Chartrand & Bargh, 1999; Stel et al., 2011; van Baaren et al., 2004), because it is necessary to (a) find the right confederate and (b) train that person to perform appropriately. Confederate features such as race, gender and age may all affect mimicry, but would be hard to control in a research setting. For example, a researcher interested in how age moderates mimicry effects could not employ a child confederate for ethical and practical reasons.

3.1.4 Robustness and statistical power. Finally, it is increasingly recognised that experimental methods in psychology may be imperfect, with weak statistical power (Chase & Chase, 1976; Cohen, 1962; Tressoldi, 2012) and possible experimenter effects (Doyen, Klein, Pichon, & Cleeremans, 2012; Klein et al., 2012). This is particularly a challenge when studying subtle social effects like mimicry and when using confederates. Our brief review of the mimicry-liking link suggest an approximate average effect size of $\eta^2 = .01$ and an average sample size of 62 participants. Most studies have used a between-subjects design, possibly to reduce participant awareness of the experimental conditions, although this is not necessarily an effective precaution (Lambdin & Shaffer, 2009). A power-analysis (G*Power) suggests that detecting an effect of $\eta^2 = .1$ with a between-groups design would require 120 participants

per group. Detecting a similar effect size with a within-subjects design would require only 22 participants (c.f. Cohen, 1992). As new factors are introduced, increasingly large participant samples must be recruited for between-subjects experiments to achieve sufficient experimental power. Between-subjects paradigms are also hard to adapt to fMRI to allow neuroimaging. Therefore, it may not be feasible to study how mimicry effects vary across different contexts and individuals using traditional between-subjects paradigms.

3.2 Future Directions: Overcoming Challenges

3.2.1 Mimicry priming. One way to avoid the difficulties with instructed mimicry is to record mimicry spontaneously occurring during interactions between two participants in a laboratory, neither of whom knows that mimicry is under investigation. In this context, video scoring of mimicry behaviours and post-session questionnaires are available to monitor the interaction, but critically the mimicry itself is generated spontaneously rather than being instructed. This method has been used to good effect in some studies (Heerey & Crossley, 2013; Heerey & Kring, 2007). However, there is little experimental control in these contexts. Priming of mimicry behaviour provides one way to improve experimental control. Priming involves the unconscious or unintentional facilitation of a particular behaviour, such as mimicry, through exposure to a particular type of stimulus or event (Molden, 2014). For example, a scrambled sentence task using prosocial concepts can lead to increases in mimicry behaviour (van Baaren, Maddux, Chartrand, de Bouter, & van Knippenberg, 2003) and automatic imitation of finger tapping movements (J. Cook & Bird, 2011; Leighton, Bird, Orsini, & Heyes, 2010), compared to sentences containing disaffiliative or antisocial words. Note that it matters in such paradigms whether priming sentences describe first-person or third-person events (Wang & Hamilton, 2013). This is consistent with other research that has reported increased levels of mimicry following unsuccessful affiliation (Lakin & Chartrand, 2003) or third party ostracism (Lakin, Chartrand, & Arkin, 2008; Over & Carpenter, 2009).

Overall, there is convergent evidence to show that mimicry is reliably increased by first-person prosocial stimuli or third-person antisocial stimuli, and the stimuli may be verbal or non-verbal. If one or both participants were primed to show more mimicry before a social interaction, both their behaviour during the interaction and their impressions afterwards could be measured. Therefore, priming could be a reliable and flexible way of manipulating mimicry within participants.

The major advantage of priming mimicry is that researchers could study the effects of mimicry as it spontaneously occurs. This is important, because the majority of empirical evidence we have about how people respond to mimicry comes from studies where mimicry was artificially instructed. We do not know to what extent behaviour in these studies diverges from true mimicry interactions where both the mimicker and mimickee are unconscious of mimicry, and therefore it is unclear how much error there is in any of the theoretical models we have outlined. Existing results could be validated or challenged using mimicry priming paradigms. Furthermore, priming would allow researchers to examine cognitive processes in both the mimicker and mimickee during a mimicry interaction, which could lead to the development of more sophisticated cognitive models that connect processes of producing mimicry and responding to mimicry.

3.2.2 Virtual mimicry. An alternative method for overcoming the challenges we outlined is to manipulate mimicry in virtual reality. Virtual reality is a popular tool for social research because people usually react to virtual characters similarly to how they would with real people (Bailenson, Blascovich, Beall, & Loomis, 2001; Donath, 2007; Garau, Slater, Pertaub, & Razaque, 2005; Reeves & Nass, 1996). Exploiting this, Bailenson & Yee (2005) developed a method for virtual mimicry. In this method, the participant wears a sensitive motion tracking device which detects the rotation of their body multiple times every second (e.g. 120 Hz), providing an accurate movement trajectory. So far, virtual mimicry studies

have only tracked head movements, but tracking could be extended to the whole body. Bailenson & Yee (2005) then programmed a virtual character to deliver a speech and mirror the participant like a reflection, with a delay of four seconds between the participant's movement and the character's movement. They suggest that delay was optimal for maximising mimicry responses while minimising detection (Bailenson et al., 2004). To achieve a control condition where the character does not mimic the participant, movement recorded from a previous participant who was being mimicked was applied to the character instead.

This method has the advantage of high control over the mimicry manipulation. Virtual characters are 'reverse engineered' (Fox, Arena, & Bailenson, 2009) to only perform the necessary behaviours, such as speaking, blinking and mimicking or not mimicking (Bailenson & Yee, 2005). The mimicry and control conditions are also well-matched, because the character is always animated with real movements made by a person being mimicked. Furthermore, the mimicry interaction can be perfectly replicated using the same computer code (Verberne et al., 2013), while characteristics of the character and the virtual environment can be endlessly tailored. For example, the researcher who wanted to investigate age could program a child character to mimic participants (Banakou, Groten, & Slater, 2013). Compared to laboratory settings, it is also more feasible to seamlessly switch between virtual characters and environments, which could avoid transparency in within-participants experiments. Finally, it may be more feasible to measure real-time responses to mimicry using virtual reality. Motion tracking devices can provide data about how people physically respond while they interact (e.g. Bailenson et al., 2008). Alternatively, researchers can play back recorded segments of the participant's virtual experience when they make ratings afterwards (C. McCall, personal communication, 4th September 2014), or even allow them to rate their experiences in real time using a virtual interface.

As well as overcoming many of the challenges associated with traditional paradigms, virtual mimicry could be used to test competing cognitive models about how people respond to mimicry. For example, to distinguish between the Contingency and Similarity models described earlier, one could program virtual characters that behave towards a participant with varying degrees of contingency and similarity. The physical similarity of the virtual mimicker to the participant could also be varied, to the extent of creating an avatar that almost perfectly resembles the participant (e.g. Osimo, Pizarro, Spanlang, & Slater, 2015), which could provide relevant data for evaluating the Self-Other Overlap model in relation to other models. Extending beyond the models described in this paper, many other potentially relevant parameters can be altered in virtual mimicry, such as the precise time delay between participant and virtual character actions.

There are some disadvantages to virtual mimicry. First, virtual mimicry tends to be an all-or-none behaviour, which cannot easily be ramped up or down within a single interaction in the same way as natural human mimicry. Second, the virtual characters must also be programmed with other aspects of natural social interaction (e.g. joint gaze) to make them socially realistic. This can be technically difficult to implement. However, the precise control of every individual social behaviour in virtual reality can be described as an advantage because it allows us to test the impact of each behaviour separately. Studies of virtual mimicry have reported similar effects to mimicry from human confederates even with minimal other behaviours (e.g. Bailenson & Yee, 2005; Verberne et al., 2013; Vrijnsen, Lange, Dotsch, et al., 2010), suggesting this can be an effective alternative approach.

3.2.3 Neuroimaging studies of mimicry. A major challenge for any neuroimaging study of mimicry is generating appropriate behaviour under controlled conditions. The participant must generate behaviour which can be mimicked, but they must also not be aware that the mimicry is occurring. However, most neuroimaging modalities require the participant

to keep still, which restricts the range of possible movements they can perform. To overcome this challenge, future neuroimaging studies could take two different approaches.

First, virtual mimicry could be combined with fMRI. Crucially, virtual mimicry paradigms involve very precise control of mimicry timing and may therefore provide suitable manipulations for fMRI. In order to translate virtual mimicry into the scanner setting, it would be necessary to use a non-magnetic motion tracking system to record the participant's movements and drive the virtual character's behaviour. Due to the sensitivity of fMRI to motion artifacts, it would also be necessary to restrict the range of head and body movement made by the participant within the scanner. Freedom of movement could be increased by using an optical tracking system to control for motion artifacts (Zaitsev, Dold, Sakas, Hennig, & Speck, 2006), or alternatively hand movements could be the target mimicry (cf. Guionnet et al., 2012). However, the constriction of the fMRI environment might also make it difficult to achieve an ecologically valid social interaction when using virtual characters.

A second option would be to combine mimicry priming or virtual mimicry with fNIRS (functional near-infrared spectroscopy). fNIRS is a non-invasive imaging technique which measures haemodynamic responses in the brain, detected using infrared light emitted by optodes fitted against the scalp. The major advantages of fNIRS over fMRI in the context of mimicry are that fNIRS is portable and much less sensitive to motion artifacts, meaning participants are able to move freely in a face-to-face interaction. A recent experiment demonstrated this possibility by using fNIRS while participants played the popular dance video game, *Dance Dance Revolution* (Noah et al., 2015). Participants also completed a version of the game adapted for fMRI, and the researchers confirmed there were equivalent activation patterns between the two methods, consistent with other cross-validations (Irani, Platek, Bunce, Ruocco, & Chute, 2007). However, participants were asked not to touch their face or head while wearing the fNIRS optodes in order to avoid face-touching artifacts; this is

a disadvantage for studies of mimicry, as face-touching is a commonly mimicked action (Cheng & Chartrand, 2003; Lakin & Chartrand, 2003; van Baaren et al., 2003). Limited depth of penetration in fNIRS also presents a major challenge for testing the possible role of the neural reward system in neurocognitive models of mimicry, because activity in regions such as the caudate and insula would not be detectable using fNIRS.

Moving forward, an optimal strategy for neuroimaging studies in this area could be to carry out complementary experiments using fMRI and fNIRS (Noah et al., 2015). Whereas fMRI could provide high spatial resolution about brain regions activated by being mimicked, fNIRS provides greater ecological validity to examine mimicry in real-world contexts. Future neuroimaging studies will be highly valuable for helping to distinguish between possible neurocognitive models for responding to mimicry, such as those we have outlined above. Due to the scarcity of neural data from participants being mimicked, we currently have to draw from neuroimaging studies which tapped into related processes such as deliberate imitation and behavioural synchrony. In order to generate an accurate model of the brain regions and cognitive processes involved in being mimicked, future research will need to exploit technological advances in virtual reality, motion tracking and neuroimaging in order to obtain data from participants during true mimicry interactions.

3.3 Summary

Progress in understanding how people respond to mimicry will require wider adoption of new methods to overcome the challenges we have highlighted. Mimicry priming and virtual reality are two potential tools for future mimicry research, which have the respective advantages of high ecological validity and good experimental control. There are already some proof-of-principle studies demonstrating the validity of these approaches. However, to address important questions about the mechanisms that produce responses to mimicry, we

will need to carry out more rigorous studies that combine highly realistic and controlled mimicry paradigms with neuroimaging techniques.

4. Unanswered Questions and Broader Scope

Finally, we turn to several major questions about mimicry which remain unanswered. We then broaden our scope to briefly consider how mimicry may be studied within a wider context of coordinated behaviour, and in development.

4.1 What is the timing of mimicry?

People's responses to mimicry have been measured at varying timescales. Temporal aspects of mimicry have received little attention (cf. Chartrand & Lakin, 2013), but could be relevant to explaining how responses to mimicry emerge. Firstly, the effects of mimicry are likely to depend on the time delay involved. In the studies we have reviewed, confederates were typically trained to mimic at delays between 2 and 5 seconds (Chartrand & Bargh, 1999; van Baaren, Decety, et al., 2009). However, the actual timing of natural or confederate mimicry is unknown. One study manipulated the time delay in virtual mimicry (1, 2, 4 or 8 seconds; Bailenson et al., 2004) and found that people were less able to detect mimicry at longer time delays. This suggests the timing of mimicry matters and people may have stronger responses to being mimicked as the time delay approaches synchrony. Evidence for stronger responses would favour the Contingency and Similarity models over the Self-Other Overlap model. Therefore, further investigation of the timing of mimicry will be important for distinguishing between different possible models of mimicry effects.

Secondly, the duration of the mimicry interaction may also be important. The effect of mimicry on liking has been tested following interactions ranging from less than a minute to over 30 minutes in duration (Table 2). There is some evidence that different mimicry effects

emerge after different durations. For instance, Verberne et al. (2013) found different results from an identical virtual mimicry algorithm experienced for different lengths of time. Fischer-Lokou et al. (2014) found that when a trained confederate mimicked participants for five minutes within a fifteen-minute negotiation task, this did not affect the outcomes of the negotiation; however, when mimicry was present throughout the negotiation task, this led to significantly more agreements and positive ratings of the negotiation. Their studies suggest that verbal mimicry may take some time to have an effect. On the other hand, some studies we reviewed have showed that unconscious behavioural mimicry significantly increases liking towards the mimicker at shorter timescales (e.g. Bailenson & Yee, 2005; Kouzakova, Karremans, et al., 2010; Stel et al., 2011). Therefore, future research will be needed to test whether people's responses to mimicry change over the course of an interaction and why some mimicry responses seem to emerge more quickly than others.

4.2 What causes conscious mimicry detection and what impact does this have?

It is unclear what causes mimicry to become consciously detected and why people respond differently when they realise they are being mimicked. Bailenson et al.'s (2004) study suggests that decreasing the time delay in mimicry increases the likelihood that people will consciously detect mimicry, but their study involved a perfect replication of the participants' movements by a virtual character, which means there may also have been a much higher degree of movement similarity compared to natural mimicry. Since no other studies have analysed data from participants who detected mimicry (Catmur & Heyes, 2013), we have very little information as to what might cause unconscious recognition of mimicry to feed into conscious awareness. Due to this lack of data, it is also unclear why the positive effects of mimicry were broken down when people became conscious of the mimicry manipulation (Bailenson et al., 2008). As Catmur and Heyes (2013) point out, participants in Bailenson et al.'s (2008) virtual mimicry study were not naïve to the possibility they would be mimicked,

and this might have contributed to their negative response. They suggest that conscious awareness of the contingent nature of mimicry may lead to negative responses. However, this speculation remains to be tested.

4.3 Does mimicry have different effects at implicit and explicit levels?

Mimicry might have different effects on implicit behaviour compared to explicit subjective feelings. This distinction was recently suggested by Hasler et al. (2014), who found that mimicry from a social outgroup member led to an increase in implicit empathy towards the outgroup in during conversation, but not in explicit ratings of warmth towards the outgroup. If mimicry effects operate differently on implicit behaviour compared to explicit feelings, this could also explain why the effects of mimicry on behavioural tasks measuring trust (Verberne et al., 2013) and persuasion (van Swol, 2003) appear to be more fragile or task-dependent (Hasler et al., 2014) than the effects of mimicry on trust and persuasion ratings. For example, the investment game (which taps into implicit trust behaviour) is sensitive to stable individual differences in trusting others (Ben-Ner & Halldorsson, 2010; Glaeser, Laibson, Scheinkman, & Soutter, 2000; Lönnqvist, Verkasalo, Walkowitz, & Wichardt, 2014), whereas ratings of trust or liking towards a specific person may be more sensitive to modulation by social characteristics such as similarity or reputation. Therefore, in future research about how people respond to mimicry, we should consider the distinction between implicit and explicit responses.

4.4 What is the relationship between different kinds of mimicry?

Many different kinds of behaviour may be mimicked beyond body movements and posture (Duffy & Chartrand, 2015). In particular, a large body of research shows that people a diverse range of behaviours like facial expressions (Bavelas, Black, Lemery, & Mullett, 1986, 1987; Dimberg, Thunberg, & Elmehed, 2000; Hsee, Hatfield, Carlson, & Chemtob, 1990), sniffing (Arzi, Shedlesky, Secundo, & Sobel, 2014) and speech (Giles & Powesland,

1975; Neumann & Strack, 2000), as well as overt choices (Harakeh, Engels, Van Baaren, & Scholte, 2007; Hermans et al., 2012; Quigley & Collins, 1999; Tanner et al., 2008; Webb, Eves, & Smith, 2011). It is not clear whether all of these different forms of mimicry reflect similar mechanisms or how they relate to one another. Our understanding of the causes and consequences of mimicry would benefit from an investigation of which neural and cognitive processes are common and distinct among different types of mimicry.

It also remains unclear how unconscious behavioural mimicry is related to behavioural synchrony. This relationship was highlighted by Chartrand and Lakin (2013). Traditionally mimicry and synchrony have been discussed in separate literatures, although each reports similar effects on liking and prosocial behaviour (Chartrand & Lakin, 2013). There also appear to be shared brain systems in responding to mimicry versus synchronised movement (Kokal et al., 2011; van Baaren et al., 2004; Wiltermuth & Heath, 2009). By definition, mimicry involves movements which match in form, whereas synchrony involves movements which match in time. However it is unclear whether this conceptual difference corresponds to differences in how people react to being mimicked compared to acting in synchrony.

4.5 Broader Scope

Throughout this review we have focused on responses to behavioural mimicry as if they were isolated phenomena, reflecting much of the empirical work in this field. Here, we wish to briefly draw attention to some broader perspectives that may yield future directions for mimicry research.

Firstly, mimicry is just one subcategory of interpersonal coordination within a dyad (Table 1). Other types of coordinated behaviour, including imitation, entrainment and synchrony, currently occupy separate research literatures. Discussions which integrate different areas of coordination literature tend to focus on similarities and differences between,

for example, mimicry and synchrony (Chartrand & Lakin, 2013; Hove & Risen, 2009; Piercarlo Valdesolo et al., 2010). This approach helps us to organise different sub-categories of coordinated behaviour. However, it is not yet known if these different sub-categories of coordinated behaviour form a single continuum dependent on the same basic neural mechanisms in all cases, or if there are clear distinctions in the cognitive and neural mechanisms for different interpersonal behaviours. For example, do imitation and complementary action draw on exactly the same systems? Are different mechanisms involved in synchrony compared to delayed imitation? Answering these questions will be important in understanding the place of mimicry in a broader social interaction context.

Secondly, mimicry can be a reciprocal process in which interaction partners switch between mimicker and mimickee roles. For practical purposes, we typically design experiments in which the participant is either mimicker or mimickee. This approach has generated a lot of research into what *causes* the mimicker to mimic, and (to a lesser extent) the downstream *consequences* of mimicry for the mimickee. However, other angles are less explored; for example, very few studies have investigated consequences of mimicry for the mimickee. Notable exceptions include studies by Inzlicht and colleagues, who have shown that mimicking outgroup members can reduce the mimicker's prejudice (Inzlicht, Gutsell, & Legault, 2012), and Stel and colleagues, who examined effects on prosocial behaviour (Stel, van Baaren, & Vonk, 2008), justice beliefs (Stel, Bos, & Bal, 2012; Stel, van den Bos, Sim, & Rispens, 2013) and lie detection (Stel et al., 2009). Moving forward, it may be beneficial to move away from the distinction between mimickers and mimickees and instead distinguish between mimicry production and mimicry perception within the same individual. This perspective is already used in research on deliberate imitation: the production and perception of imitation can be seen to co-develop in children (e.g. Eckerman & Stein, 1990; Nadel-Brulfert & Baudonniere, 1982; Nadel, 2014), and have been studied together in the same

individual during neuroimaging studies (Brass et al., 2009; J. Decety et al., 2002; Guionnet et al., 2012). If we were to apply a similar perspective to mimicry research, this might give us a clearer insight into common and distinct cognitive mechanisms involved in mimicking and responding to mimicry. One way to implement this approach could be through priming participants in a dyad to unconsciously mimic one another in turns.

Finally, mimicry and other aspects of interpersonal coordination continue to develop from infancy to adulthood. Traditionally, mimicry has been investigated separately in infants and adults (although much of the infant research looks at adult-infant dyads), and there has been little exploration of how mimicry develops during childhood and adolescence. Our understanding of mimicry may benefit from a more joined-up view of mimicry development, especially with regards to the relationship between mimicry production and mimicry perception. In infant research, the ‘like-me’ theory suggests that mimicry perception develops on an innate capacity to mimic others (Meltzoff, 2007a, 2007b), whereas the competing ‘me-like-you’ theory relies on mimicry perception to explain how that infants derive an understanding of themselves from others (Prinz, 2012). We may make progress in debates such as this one with a research agenda that bridges infant and adult mimicry.

Conclusions

Current research focusing on the mimicker is beginning to uncover complexities in people’s neural and cognitive responses to being mimicked. In behavioural research, a wide variety of positive responses to mimicry have been reported. However, links from mimicry to liking, trust and other positive outcomes appear to be fragile. Recent studies have revealed that positive responses to mimicry can break down in certain individuals and social situations

where mimicry may be unexpected. Thus, a complex range of factors may determine how a given individual responds to mimicry in a given context.

In addition to this range of factors, neuroscientific research shows that several brain systems are activated in response to mimicry, including regions associated with mirror properties, self-other processing and reward. However, the volume of data is very small, and it is unclear how these neural systems relate to the range of effects found in behavioural studies. We have outlined three potential models linking neural and cognitive responses to mimicry, which suggest that positive downstream consequences of mimicry may depend upon self-other overlap, detection of contingency or low prediction error. Each of these models receives partial support from behavioural data. A key area for future research will be to develop models which successfully explain neural and behavioural data. With the advance of imaging technologies such as NIRS, it may become more feasible to study neural responses in live social interactions.

In order to reach a detailed neurocognitive understanding of how people respond to mimicry, researchers will also need to overcome limitations with traditional research designs. Alternative approaches to using confederate mimickers may open up new opportunities to achieve highly realistic and controlled experiments. We have outlined the advantages of unconsciously priming participants or programming virtual characters to mimic. In addition, future studies must have enough power for detecting subtle mimicry effects. If we focus on selecting appropriate methodologies, we may be able to address open questions which have so far been difficult to study, and embed theories of mimicry within a broader understanding of behavioural coordination.

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Figure Captions

Figure 1. Brain regions associated with being mimicked. Unconscious recognition of a perception-action match during mimicry may be associated with MNS activity. Being mimicked increases self-other processing, which may be linked to activity in TPJ and right inferior parietal cortex. Being mimicked is also associated with increased functional connectivity between vmPFC and striatum/insula. Increased activity in striatum and insula may reflect reward and positive responses to being mimicked. The Self-Other Overlap, Contingency and Similarity models predict different cognitive pathways connecting these brain regions.

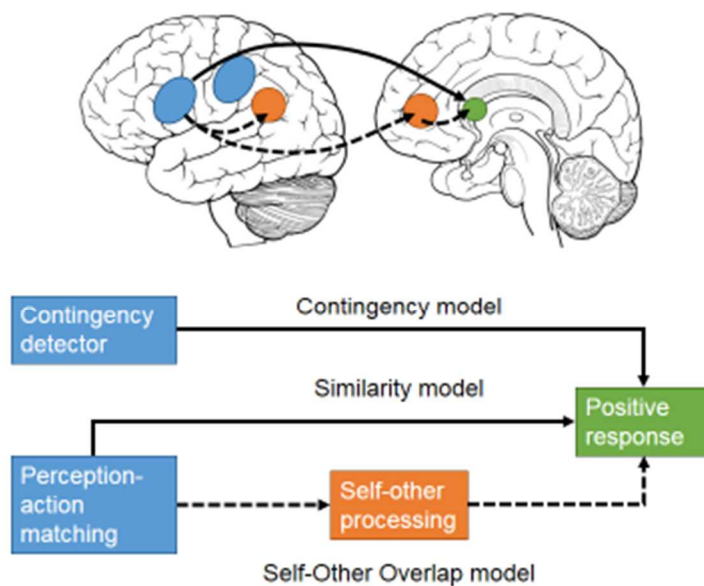


Table 1. Definitions.

General terms		
<i>Interpersonal coordination</i>		
The degree to which the behaviours in an interaction are nonrandom, patterned, or synchronised in both timing and form (Bernieri & Rosenthal, 1991).		
	Synchrony in timing	Delay in timing
	<i>Entrainment</i> The behaviour of two moving actors A1 and A2 becomes coupled because they mutually affect each other's behaviour (Knoblich & Sebanz, 2008).	<i>Contingency</i> The extent to which activation of one representation predicts activation of another (Cook et al., 2010).
Same form	<i>Perfect synchrony</i> The matching of behaviour in both form and time (Miles et al., 2010), e.g. marching in parade.	<i>Imitation</i> Copying the form of an action (Whiten et al., 2009). Imitation is volitional (Kinsbourne & Helt, 2011) and goal-directed (Bekkering et al., 2000).
		<i>Mimicry</i> The automatic imitation of gestures, postures, mannerisms, and other motor movements (Chartrand & Bargh, 1999). Mimicry is not goal-directed (Hamilton, 2008).
Different form	<i>General synchrony</i> The matching of different behaviours at the same time, e.g. playing of an orchestra.	Complementary actions and other non-matching contingent behaviours, e.g. taking an object from someone's hand.

Table 2. Studies measuring the effect of mimicry on liking.

Reference	Experimental design	Social interaction task	Mimicry condition	Control condition	Mimicry duration	Measure of liking	Participants (N)	Reported effect size	Significance (p)
Baileenson & Yee (2005)	Between-participants	Persuasive speech	Virtual character mirrored participant head movement	Virtual character displayed previous participant head movement	195 seconds	Agent impression: 13 items ^a , including 9-point scale <i>Not at all likeable – Very likeable</i>	69	Not reported	<.001
Drury & van Swol (2005)	Between-participants	Debate	Confederate mirrored participant body posture and movement	Confederate moved naturally while avoiding movement related to the participant's movement	10 minutes	7-point scale <i>Not likeable -Likeable</i>	78	$\eta^2 = 0.01$.90
Kouzakova, Karremans et al. (2010)	Between-participants	Mundane tasks, e.g. describing photos and naming	Confederate mirrored participant body posture and	Confederate moved naturally while avoiding movement synchronous with the	5 minutes	7-point scale (<i>Likeability</i>)	69	.11	$\eta^2 = .03$

		depicted animals	movement	participant's movement				$\eta^2 =$	
Kouzes	Betw	Mundan	Confede	Confederate	5	7-point	40		.03
akova	een-	e tasks	rate mirrored	moved naturally while	minutes	scale (<i>Likeability</i>)		.12	
Karremans et al. (2010)	participants		participant body posture and movement	avoiding movement synchronous with the participant's movement					
Kouzes	Betw	Mundan	Confede	Confederate	10	7-point	72	$\eta^2 =$.004
akova, van	een-	e tasks	rate mirrored	moved naturally while	minutes	scale		.12	
Baaren et al. (2010)	participants		participant body posture and movement	avoiding movement synchronous with the participant's movement		<i>Not at all</i> – <i>Very much</i> (<i>Likeable</i>)			
Stel	Betw	Descript	Confede	Confederate	3	7-point	88	$\eta^2 =$.01
et al. (2011)	een-	ion of film fragment	rate mimicked	avoided mimicry	minutes	scale		0.10	
	participants		participant body posture and movement	while keeping other behaviour constant		<i>Did you like your interaction partner? Did you get along with your interaction partner?</i>			

	Stel	Betw	Giving	Confede	Confederate	43	7-point	Pros	Pros	Pros
et al. (2011)	een-	transport	rate mimicked	avoided mimicry	seconds	scale	elf:	elf:	elf:	
	participants	directions	participant body posture and movement and vocal and facial expressions	while keeping other behaviour constant	(average)		<i>Did you like your interaction partner? Did you get along with your interaction partner?</i>	22	Not reported	n.s.
								Pros		Pros
								27	ocial:	ocial:
									$\eta^2 =$.05
									0.08	
	Verb	Betw	Task	Virtual	Virtual	Tria	Liking: 13	40	Tria	Tria
erne et al. (2013)	een-	instructions	character mirrored participant head movement	character displayed previous participant head movement	1 1:	102	items ^a , including 7-point scale	1 1:	1 1:	>
	participants				seconds		<i>Totally disagree – Totally agree (Likeable)</i>	reported	.131	
									Tria	Tria
					1 2:			1 2:	1 2:	
					Not reported				η_p^2	.027
								= .13		

Mad dux et al. (2008)	Between- participants	Negotiation	Other participant instructed to mimic participant movements	Other participant not instructed to mimic	45 minutes	5-point scale	62	Not reported	> .23
							<i>How much did you like negotiating with the other person?</i>		
							<i>Not at all</i>		
							<i>– very much</i>		
van Swol (2003)	With in-participants	Debate	Confederate rate mirrored participant body posture and movement from waist up	Confederate moved naturally while avoiding movement related to the participant's movement	10- 12 minutes	7-point scale	54	Cohen's d = .62	.64
							<i>Not likeable -Likeable</i>		

^aOriginal items can be found in Guadagno & Cialdini (2002)

Table 3. Neuroimaging results for regions that respond to being mimicked.

Reference	Imaging method	Social interaction task	Conditions	Participants (N)	Contrast	Regions activated	Coordinates (x, y, z)
Decety et al. (2002)	ET	Participants used their hands to move three small objects into a configuration. They were shown their own movements or similar actions by an experimenter over video link.	<ul style="list-style-type: none"> • Participant imitates experimenter, • Experimenter imitates participant, • Participant watches own actions, • Participant watches experimenter's actions 	18	Experimenter > Participant imitates participant imitates experimenter	R medial frontal gyrus R supramarginal gyrus R middle frontal gyrus R inferior temporal gyrus L pre-SMA L posterior cingulate L medial frontal	20, 24, 40 56, -46, 28 28, 40, 18 66, -52, -12 24, 12, 66 -12, -70, 44

gyrus -12,
 L anterior cingulate 20, 38
 L orbital gyrus 24,
 28, 20
 -18,
 -52, 20

Br	f	Participants		20	Be imitated	TPJ (ROI analysis	52, -
ass et al.	MRI	completed an	<ul style="list-style-type: none"> • Simultaneously imitate • Simultaneously counter-imitate • Be imitated after a delay • Be counter-imitated after a delay 		after a delay	only)	54, 21
(2009)		imitation-inhibition			>		
		task in which they had			Simultaneously		
		to execute index or			imitate		
		middle finger					
		movements and					
		observed video stimuli					
		of congruent or					
		incongruent					

movements.

Kuhn et al. (2010)	f	<p>Participants watched pseudo-first-person perspective videos of one person interacting with various interaction partners. The person's hand and leg movements were mimicked or anti-mimicked by their interaction partner.</p>	<ul style="list-style-type: none"> • Mimicry • Antimimicry 	15	<p>Mimicry > Anti-mimicry</p>	<p>mOFC/vmPFC (BA 10)</p>	<p>-7, 49, -7</p>
Ko	f	Participants	<ul style="list-style-type: none"> • Synchrony • Asynchrony 	18	Synchrony >	L post central	-52,

kal et al. (2011)	MRI	completed a drumming task with two experimenters outside the scanner. One experimenter drummed in synchrony with them and the other drummed out of synchrony. Baseline was taken during random pauses between drumming trials.	• Baseline	Baseline	gyrus R inferior frontal gyrus L medial temporal gyrus R cerebellar vermis III R SMA R post central gyrus (BA 4p) STG L post central gyrus (BA 2) R IPL R superior medial gyrus	-16, 40 52, 6, 14 -54, -38, 8 2, - 36, -16 4, -2, 52 38, - 26, 52 50, - 14, 4 -42, 32, 42 44, -
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L pallidum	46, 48
R pallidum	54, -
R caudate	34, 42
R thalamus	-20,
L thalamus	4, 2
L putamen	20, -
	6, -4
	14,
	6, 8
	12, -
	12, 4
	-12,
	-14, 4
	-18,
	4, 8

Guionnet et al. (2012)	fMRI	Participants interacted with an experimenter outside the scanner by making hand gestures over video link. In one condition, gesture matching was freely co-regulated by the interactors. In another condition, the experimenter or participant was instructed to imitate.	<ul style="list-style-type: none"> • Experimenter freely imitates participant • Participant freely imitates experimenter • Experimenter instructed to imitate participant • Participant instructed to imitate experimenter 	23	Be imitated > Imitate (collapsed across free and instructed conditions)	dACC (BA 32) dACC (BA 24) left anterior insula	-2, 22, 38 6, 24, 28 -38, 18, 0
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