

Automatic Imitation

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“Automatic imitation” is a type of stimulus-response compatibility effect in which the topographical features of task-irrelevant action stimuli facilitate similar, and interfere with dissimilar, responses. This article reviews behavioral, neurophysiological, and neuroimaging research on automatic imitation, asking in what sense it is “automatic” and whether it is “imitation.” This body of research reveals that automatic imitation is a covert form of imitation, distinct from spatial compatibility. It also indicates that, although automatic imitation is subject to input modulation by attentional processes, and output modulation by inhibitory processes, it is mediated by learned, long-term sensorimotor associations that cannot be altered directly by intentional processes. Automatic imitation provides an important tool for the investigation of the mirror neuron system, motor mimicry, and complex forms of imitation. It is a new behavioral phenomenon, comparable with the Stroop and Simon effects, providing strong evidence that even healthy adult humans are prone, in an unwilling and unreasoned way, to copy the actions of others.

Keywords: imitation, automaticity, mirror neuron system, motor mimicry, stimulus-response compatibility

In a Victorian parlor game similar to “Simon Says,” eager young children sat around a tea table as the *pater familias* issued stern commands to “hold tight” or “let go” of the tablecloth (Squareman, 1916). While speaking each command, the adult performed a compatible or incompatible action. For example, while saying “hold tight,” he either grasped or released the tablecloth. When the adult’s action was incompatible with his command, any child who imitated the action, rather than obeying the command, went out of the game. Those unlucky children were caught out by what has come to be known as “automatic imitation”—a tendency to copy observed actions when they are not relevant to the task at hand and when copying can interfere with performance.

Experimental evidence that healthy adults are susceptible to automatic imitation began to emerge in the mid-1990s (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Stürmer, Aschersleben, & Prinz, 2000), and there are now more than 75 published experiments investigating the phenomenon. The evidence comes from studies using a special kind of stimulus-response (S-R) compatibility (SRC; Proctor & Vu, 2006) procedure, in which the stimulus set includes photographic images of the actions in the response set. For example, in one of the original studies, Stürmer et al. (2000) asked participants to open and close their hands in response to a color cue (red or blue; the “task-relevant” stimulus dimension) superimposed on a video of an opening or closing hand (the “task-irrelevant” stimulus dimension). Correct responses were initiated faster when the irrelevant

action stimulus was response-compatible (i.e., when an open hand response was made in the presence of an opening hand stimulus, and a close hand response was made in the presence of a closing hand stimulus) than when the irrelevant action stimulus was response-incompatible (i.e., when an open hand response was made in the presence of a closing hand stimulus, and a close hand response was made in the presence of an opening hand stimulus). In other words, response times (RTs) were shorter in compatible than in incompatible trials. Subsequent studies have reported similar, robust effects for a range of finger, hand, arm, foot, and mouth actions.

Effects of this kind have been given a variety of names, including “motor priming” (Liepelt, von Cramon, & Brass, 2008), “visuomotor priming” (Craighero et al., 1996), “body part priming” (Bach & Tipper, 2007), “effector priming” (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008), “imitation inhibition” (Brass, Derrfuss, & von Cramon, 2005), “imitative compatibility” (Catmur & Heyes, in press), “movement compatibility” (Brass et al., 2000), “movement interference” (Gowen, Stanley, & Miall, 2008), “motor facilitation by action observation” (Edwards, Humphreys, & Castiello, 2003), and “motor mimicry” (Spengler, Brass, Kuhn, & Schutz-Bosbach, 2010). However, the term “automatic imitation,” which is now in common use (Heyes, Bird, Johnson, & Haggard, 2005; Liepelt & Brass, 2010; Longo & Berthenthal, 2009; Longo, Kosobud, & Berthenthal, 2008; Press, Bird, Walsh, & Heyes, 2008), captures two substantial, widely held and apparently paradoxical assumptions about the phenomenon: that it is relatively independent with respect to the actor’s intentions, and yet is related in an important way to the deliberate copying of observed body movements. Drawing on the entire literature to date (as revealed by PsycINFO and Google Scholar databases, systematic scrutiny of the reference lists in published articles, and direct enquiries about unpublished work), this review tests these assumptions. It asks to what extent and in what ways automatic imitation is unintended and how, if at all, it is related to the intentional reproduction of

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observed body movements. In short, the present review asks whether “automatic imitation” is “automatic” and whether it is “imitation.”

These questions are important in relation to issues both of enduring significance and of particular current interest in psychological science. One of the most enduring issues in psychology and philosophy concerns the extent to which behavior is controlled by reason and “the will.” Since the inception of experimental psychology, this question has been examined in contexts where people are like machine operators—reacting to arbitrary stimuli and seeking to control events in the inanimate environment. In common with this kind of research on action control, research on automatic imitation uses tightly controlled experimental methods. However, in the case of automatic imitation, these procedures examine the extent to which social rather than inanimate stimuli—the actions of other people—influence our behavior in ways that are not willed and that are outside the “space of reasons” (Sellars, Rorty, & Brandom, 1997).

Another issue of enduring interest concerns the status of imitation. Since the scientific study of imitation began in the late 19th century, it has been interpreted in two radically different ways. On the one hand, imitation has been viewed as a sophisticated cognitive process, essential for human development and enculturation (Washburn, 1908), and on the other hand, as a blind, brutish and irrational force in human affairs (Darwin, 1871). This could be because there are in fact two radically different types of imitation: a complex, intentional type of imitation, enabling the acquisition of novel behavior, and a simple, involuntary variety, involving nothing more than the duplication of familiar actions (Heyes, in press; Tomasello, 1996). However, research on automatic imitation has raised an alternative possibility—that “complex” imitation and “simple” imitation are mediated by the same psychological mechanisms and, therefore, that “simple” automatic imitation can be used to find out how “complex” intentional imitation is mediated (Heyes, 2005).

Turning from perennial to topical issues, automatic imitation is currently of interest because it lies at the intersection between fascinating recent developments in cognitive neuroscience and experimental social psychology. The former relate to the discovery of “mirror neurons” or the “mirror neuron system”—areas of the premotor and inferior parietal cortex that are active during the execution of specific actions and during passive observation of the same actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni, 2009). The latter developments provide compelling evidence that, in everyday life, people engage in a great deal of spontaneous “behavioral” or “motor mimicry” and that this activity has a major impact on cooperative attitudes and behavior (see Chartrand & Van Baaren, 2009, for a recent review). Many researchers believe that automatic imitation is mediated by the mirror neuron system (Longo et al., 2008) and that motor mimicry is automatic imitation “in the wild”—the same psychological phenomenon, detected under naturalistic rather than tightly controlled experimental conditions (Chartrand & Van Baaren, 2009). If this is correct, research on automatic imitation has the potential to play a crucial role in elucidating the psychological functions of the mirror neuron system and in explaining exactly how imitating and being imitated promotes prosocial behavior. However, these relationships—between the mirror neuron system, automatic imitation, and motor mimicry—have not yet been demonstrated. The

mirror neuron system is widely believed to connect action perception with action production in a “direct” way—without, for example, the mediation of higher cortical processes (but see, e.g., Csibra, 2008)—and motor mimicry is thought to be unconscious and unintentional. Therefore, if “automatic imitation” is not also direct and unintentional—if it is not automatic—it is unlikely to be either mediated by the mirror neuron system or a laboratory model of motor mimicry. Similarly, at the heart of the mirror neuron system and motor mimicry are fundamentally imitative relations; in both cases, what are matched across perception and action are the configurational or “topographical” properties of body movements—the way in which parts of the body move relative to one another. Therefore, if “automatic imitation” is not really a form of imitation, if it does not also depend on topographical features of body movements, automatic imitation will not be able to bridge the gap between the bench neuroscience of the mirror neuron system and the real world relevance of motor mimicry.

This review begins with a brief overview of methods that have been used to investigate automatic imitation and by distinguishing automatic imitation from phenomena associated more directly with the mirror neuron system, that is, “mirror effects,” and from motor mimicry. Following this groundwork, the article is divided into three principal sections. The first asks whether “automatic imitation” is imitation, and the second asks whether it is automatic. The imitation question is addressed first because it raises a fundamental concern: that automatic imitation may be nothing more than a spatial compatibility effect produced by action stimuli. In other words, in automatic imitation paradigms, performance may be affected by simple (e.g., left-right, top-down) spatial properties, rather than topographical features, of the irrelevant action stimuli. Therefore, to identify studies that can provide information about the automaticity of automatic imitation, it is first necessary to establish which experimental procedures can be trusted to dissociate automatic imitation from spatial compatibility. Following this demonstration that automatic imitation is indeed “imitation,” the section on automaticity examines the extent to which automatic imitation is independent of intention. More specifically, it considers whether intentional processes can intervene to prevent or divert automatic imitation. In combination, the sections on imitation and automaticity find evidence that automatic imitation is mediated by unintended activation of durable connections between sensory and motor representations of the topographic features of action. The third major section of the article examines the origins of these long-term connections and reviews evidence that they are products of learning. The final section summarizes the review’s findings and their implications for future research on automatic imitation, the mirror neuron system, and motor mimicry.

Three Related Phenomena

Automatic Imitation

Operationally defined, *automatic imitation* is a species of SRC effect in which the speed and/or accuracy of behavioral performance is modulated by the relationship between the topographic features of task-irrelevant action stimuli and the participant’s responses. SRC protocols have been used for many years to investigate action representation and control (Simon, 1969; Stroop, 1935). Using RT and error measures, they assess the impact on

performance of stimuli that are similar (compatible) or dissimilar (incompatible) to the executed action on one or more dimensions. Two of the seminal studies of automatic imitation each used a choice reaction time SRC procedure in which the compatible and incompatible cues were photographic images of another person performing the actions in the response set (Brass et al., 2000; Stürmer et al., 2000). These cues were task-irrelevant; participants were not required to attend or respond to them to comply with task instructions.

The study by Stürmer et al. (2000) examined hand opening (extending and splaying the fingers away from the palm) and hand closing (rolling the fingers into a fist). These actions are intransitive (they do not involve an inanimate object) and antagonistic (it is not possible to perform both actions at the same time). In each trial, participants viewed one of the two hand actions, from the first person perspective, on a computer screen. At the moment when the hand stimulus started to move, or shortly afterwards, the hand changed abruptly from flesh color to either blue or red. Participants were instructed to respond as quickly as possible to this color change by either opening or closing their own hand. They were required to open their hand in response to the blue stimulus and to close it in response to the red stimulus, or vice versa. Although the observed action (open or close) was task-irrelevant, responses were faster when the action of the stimulus hand was compatible with the correct response (e.g., open hand stimulus and open hand response) than when the stimulus action was response-incompatible (e.g., close hand stimulus and open hand response). This effect was observed with both dynamic action stimuli (videos) and static action stimuli (stills depicting the movement endpoint). It indicated that observation of the same action facilitated responding in compatible trials and/or that observation of the alternative action interfered with responding in incompatible trials.

In the other study, Brass et al. (2000) examined lifting movements of the index and middle fingers. These actions are transitive, in that they relate to the surface of an environmental object, and nonantagonistic (it is possible to perform both actions at the same time). In each trial, participants first saw, from a third party perspective, a hand with fingers curled downward and each fingertip resting on a table. Shortly afterwards, a number (1 or 2) appeared between the fingers, and participants were required to lift their index finger in response to the number 1 and their middle finger in response to the number 2, or vice versa. In baseline trials, the stimulus hand did not move when the number was presented. In all other trials, the appearance of the number coincided with lifting of either the index or the middle finger of the stimulus hand. Responses were faster when the stimulus action was the same as the correct response (compatible trials, e.g., index finger stimulus and index finger response) than in baseline trials, and responses in baseline trials were faster than when the stimulus action differed from the correct response (incompatible trials, e.g., middle finger stimulus and index finger response). This suggested that "movement observation exerts an automatic influence on movement execution" (Brass et al., 2000, p. 139) and that this automatic influence both facilitates responding in compatible trials and interferes with responding in incompatible trials.

The automatic imitation effects reported by Stürmer et al. (2000) and Brass et al. (2000) have been replicated many times, and similar effects have been found, also using choice RT procedures, for other pairs of actions. Foot movements are initiated faster

(Gillmeister et al., 2008) and performed more accurately (Bach & Tipper, 2007) while observing task-irrelevant foot movements than while observing task-irrelevant hand movements, and vice versa. Index and little finger abduction are initiated faster when the imperative stimulus (a colored dot) is presented with a response-compatible rather than a response-incompatible finger movement (index or little finger abduction; Catmur & Heyes, in press), and opening and closing mouth responses to letter and color stimuli are faster when the imperative cue is accompanied by a task-irrelevant image of the same action than by an image of the alternative action (Leighton & Heyes, 2010).

Automatic imitation effects have also been found in simple RT tasks, where the participant performs the same prespecified response in every trial within a block, cued by the onset of a stimulus action (the go-signal). Adapting the procedure used by Stürmer et al. (2000), Heyes et al. (2005) found that hand opening and closing responses were initiated faster when they were cued by the onset of compatible rather than incompatible hand movement stimuli (e.g., an open hand response cued by an open, rather than a closed, hand stimulus). Likewise, Brass, Bekkering, and Prinz (2001) reported that lifting and tapping movements of an index finger were faster when they were cued by response-compatible rather than response-incompatible stimuli (e.g., a lifting response cued by a lifting, rather than a tapping, stimulus), and horizontal and vertical arm movements are performed less accurately when participants are simultaneously observing arm movements in the incompatible plane (Gowen et al., 2008; Kilner, Hamilton, & Blakemore, 2007; Kilner, Paulignan, & Blakemore, 2003).

The foregoing studies suggest that when people are engaged in a task requiring them to respond to a cue by performing a particular action, A, observation of A can facilitate and observation of an alternative action, B, can interfere with performance, even when the observed action is task-irrelevant. Effects of this kind, detected using SRC procedures, provide the core examples of automatic imitation and are the focus of this article. However, I also refer to two other classes of phenomenon: "mirror effects" and "motor mimicry." Like automatic imitation, these phenomena suggest that action observation activates processes involved in action execution and that this activation is minimally dependent on the observer's intentions.

Mirror Effects

Mirror effects differ from automatic imitation effects in that they (a) are detected using neurophysiological rather than behavioral measures and (b) occur when participants passively observe body movements, that is, when participants are required only to observe a stimulus display or to respond with actions of a different type from those observed.

The mirror effects most closely related to automatic imitation indicate that action observation selectively activates the muscles involved in performing the observed action. For example, Berger and Hadley (1975) reported that observers show more electromyographic (EMG) activity in the arm while observing arm wrestling than while observing stuttering, and greater EMG activity in the lips when observing stuttering than while observing arm wrestling. More recent studies, measuring transcranial magnetic stimulation (TMS) induced motor evoked potentials (MEPs), have reported similar effects during the observation of arm and hand movements

(Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000) and movements of the index and little fingers of the right hand (Catmur, Walsh, & Heyes, 2007). Like core examples of automatic imitation, the latter effect was event-related. Rather than being blocked, the index and little finger movements were presented in random order across trials. Therefore, Catmur et al. (2007) showed that a single presentation of a movement stimulus is sufficient to produce mirror muscle-specific activation; it is not necessary for the same movement stimulus to be observed repeatedly.

EMG has also been used to detect mirror effects involving facial expressions of emotion, including anger and happiness (Dimberg, Thunberg, & Elmehed, 2000). However, it is difficult to establish whether these effects represent a direct influence of observed action on executed action or are mediated by emotional states induced by the action stimuli (Cannon, Hayes, & Tipper, 2009; Hess & Blairy, 2001).

Studies using functional magnetic resonance imaging (fMRI) and positron emission tomography show that the cortical areas active during action observation overlap with those that are active during execution of the same class of actions. The areas of overlap include the inferior frontal gyrus (e.g., Iacoboni et al., 1999; Kilner, Neal, Weiskopf, Friston, & Frith, 2010), the ventral and dorsal premotor cortex (Buccino et al., 2004; Gazzola, Rizzolatti, Wicker, & Keysers, 2007), the inferior parietal lobe (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Grèzes, Armony, Rowe, & Passingham, 2003), the anterior intraparietal sulcus (Dinstein, Hasson, Rubin, & Heeger, 2007; Shmuelof & Zohary, 2006), and the superior temporal sulcus (Gazzola, Aziz-Zadeh, & Keysers, 2006). Single-unit recording indicates that monkeys have mirror neurons in some of these areas, that is, individual cells that fire during observation and execution of the same action. Consequently, the areas of the human brain that are activated by observation and execution of the same actions are sometimes called the “mirror neuron system.”

There has been a great deal of speculation about the cognitive functions of the mirror neuron system—linking it with action understanding, empathy, theory of mind, language comprehension, imitation, and a range of other cognitive functions—but there has been very little experimental work testing these hypotheses. In this spirit, many researchers assume that automatic imitation is mediated by the mirror neuron system and, therefore, that the magnitude of automatic imitation effects can be used as an index of mirror system functioning (Kilner et al., 2003; Longo et al., 2008; Press, Bird, Flach, & Heyes, 2005; Stanley, Gowen, & Miall, 2007; van Schie, van Waterschoot, & Bekkering, 2008). For example, evidence that automatic imitation effects are as great in people with autism spectrum conditions (ASC) as in typically developing controls (Bird, Leighton, Press, & Heyes, 2007; Gowen et al., 2008; see also Bach, Peatfield, & Tipper, 2007) has been taken to indicate that ASC is not characterized by an impairment of the mirror neuron system (contra, e.g., Williams et al., 2006). However, only one study has provided evidence of a causal relationship between the mirror neuron system and automatic imitation (Catmur, Walsh, & Heyes, 2009). This study showed that disruptive, theta burst TMS of the inferior frontal gyrus selectively impaired automatic imitation of index and little finger abduction movements.

Motor Mimicry

In contrast with automatic imitation, motor mimicry is detected (a) in naturalistic social situations (e.g., when a participant is in conversation with a confederate) and (b) via measures of action frequency within a session rather than measures of speed and/or accuracy within trials. For example, Chartrand and Bargh (1999) observed each participant for two sessions in which the participant described photographs with a confederate. In one session, the confederate repeatedly touched her face, and in the other session, she repeatedly moved her foot. Hidden cameras showed that in the session with the face-touching confederate, participants touched their faces more often than they moved their feet, and in the session with the foot-moving confederate, participants moved their feet more often than they touched their faces. A number of studies have shown that motor mimicry of this kind both promotes and is promoted by prosocial attitudes and behavior (see Chartrand & Van Baaren, 2009, for a review). For example, people who have been mimicked report greater rapport (Chartrand & Bargh, 1999), feelings of closeness (van Baaren, Holland, Kawakami, & van Knippenberg, 2004), affiliation (Hove & Risen, 2009), and trust (Baileson & Yee, 2005) toward the mimicking social partner, and individuals who are liked, or identified as in-group members, are mimicked with a higher frequency than disliked individuals and out-group members (Likowski, Muhlberger, Seibt, Pauli, & Weyers, 2008; Stel et al., 2010). The evidence that motor mimicry occurs without the mimicker intending to copy the actions of the mimicked comes from posttest interviews in which participants do not report awareness of the model's focal behavior (e.g., foot moving, face rubbing), an intention to mimic, or awareness that they mimicked the confederate's behavior (Chartrand & Bargh, 1999).

There has been very little integration of research on motor mimicry and automatic imitation. Consequently, although it is plausible that these phenomena depend on the same psychological and neural processes, this has yet to be confirmed. Preliminary evidence comes from studies showing that social priming has similar effects on motor mimicry (Lakin & Chartrand, 2003; van Baaren, Maddux, Chartrand, De Bouter, & van Knippenberg, 2003) and automatic imitation (J. Cook & Bird, 2010b; Leighton, Bird, Orsini, & Heyes, 2010). For example, in a hand opening/closing simple RT procedure, participants who had just completed a scrambled sentence task containing prosocial words (e.g., affiliate, friend, cooperate) showed a larger automatic imitation effect (RT on incompatible trials minus RT on compatible trials) than participants who had just completed a scrambled sentence task containing antisocial words (e.g., rebel, independent, individual; Leighton et al., 2010).

In conclusion, the similarities between automatic imitation, mirror effects, and motor mimicry have led some researchers to propose that automatic imitation is mediated by the mirror neuron system and that it is a tightly controlled laboratory equivalent of the motor mimicry observed in naturalistic social contexts. If these hypotheses are correct, then automatic imitation can be used as a tool to investigate how the mirror neuron system contributes to cognitive functioning and how motor mimicry promotes prosocial attitudes and behavior. However, to validate these hypotheses, it is necessary to establish that, in common with mirror effects and

motor mimicry, “automatic imitation” is both unintentional and a form of imitation.

Is “Automatic Imitation” Really Imitation?

The term “imitation” is commonly used to refer to cases in which an individual, having observed a body movement, deliberately performs a topographically similar body movement (Heyes, 2001). For example, as a result of having seen you splay your fingers, I may splay my fingers. The topographic similarity of two actions varies with the degree to which they involve the same spatial relationships among parts of the actor’s body. Thus, my splaying movement and your splaying movement are topographically similar to one another, and distinct from making a fist, in that they both involve separating the fingers and extending them away from the palm.

Imitation is often contrasted with “emulation” (Tomasello, 1996) and with “spatial compatibility” (Brass, Bekkering, & Prinz, 2001). In emulation, action observation promotes the performance of an action that is similar, not in its body movement topography, but in its effects on an environmental object. As a result of seeing you tip a bucket, I may also tip a bucket, but while you rotated the object in your hands, I kick it with my foot. A third type of matching or similarity is involved in spatially compatible responding. In this case, the observer responds in the same relative position as the actor but not necessarily using the same response topography or effecting the same object transformation. In a cloak-room, seeing you hang your coat on an upper rather than a lower hook might prompt me to select an upper rather than a lower shelf on which to place my bag.¹

Automatic imitation appears to be rather different from canonical examples of imitation. “Imitation” typically refers to overt behavioral execution of actions similar to those observed, but automatic imitation rarely involves overt behavioral execution of matching responses. Automatic imitation effects typically consist of RT, rather than accuracy, differences between compatible and incompatible trials. Actions are initiated faster while observing similar rather than dissimilar actions, but participants only occasionally make the mistake of actually performing the observed rather than the instructed action. Therefore, if it is any kind of imitation at all, automatic imitation is a covert form of imitation—related to imitation in much the same way that silent reading is related to reading aloud. In other words, automatic imitation may be a phenomenon generated by the same core process as overt behavioral imitation but in which the impulse or capacity to copy an action is not fully expressed.

It is generally agreed that automatic imitation effects result from a process in which action observation activates motor representations that are “similar” to the action observed. To find out whether automatic imitation is really a covert form of imitation, we need to know in what respect these motor representations are similar to their eliciting stimuli. Topographic similarity between observed and executed action is characteristic of overt behavioral imitation. Therefore, there will be a strong case for regarding automatic imitation as a covert form of overt behavioral imitation only if automatic imitation effects are due to the activation by action observation of motor representations that code topographically similar body movements. If the motor representations activated by action observation code similar object transformations (Tucker &

Ellis, 1998), it would be more appropriate to speak of “automatic emulation” than “automatic imitation.” If they code the same relative spatial positions (e.g., up vs. down, or left vs. right), “automatic imitation” is merely a type of spatially compatible responding in which the spatial stimulus happens to be presented in the form of a body movement.

Imitation Versus Emulation

A number of studies have shown that observing a task-irrelevant object, rather than a task-irrelevant action, can influence the performance of an instructed action on a similar object (Craighero et al., 1998, 1996; Edwards et al., 2003; Tucker & Ellis, 1998). For example, Edwards et al. (2003) required participants to reach and grasp a large or small circular object immediately after they had observed an object of the same size (compatible trials) or of a different size (incompatible trials). In one condition, participants simply observed the object, and in another condition, they observed both the object and the experimenter reaching and grasping the object. Time to peak grasp aperture was shorter in compatible than in incompatible trials, and this effect was no greater after observing action on the object than after observing the object alone.

These findings remind us that, in principle, automatic imitation could be confused with automatic emulation. When a participant observes a body movement applied to an object, it could be features of the object (e.g., size, orientation), rather than features of the body movement, that prime a corresponding motor representation. However, very few effects currently understood to be examples of automatic imitation could be due instead to automatic emulation. This is because the vast majority of experimental designs used to detect automatic imitation do not confound body movements with object properties. In many cases, the stimulus and response body movements are intransitive (e.g., hand opening and closing, index and little finger abduction, horizontal and vertical arm movements), and in experiments where body movements are related to an object, the properties of the object do not vary with those of the body movement (e.g., finger lifting and tapping). The exceptional cases are studies, designed to promote ecological validity, that use different movements applied to different parts of an object (Ocampo & Kritikos, 2010; van Schie et al., 2008)—for example, power grip applied to the bowl of a wine glass, and precision grip applied to the stem. With these exceptions, we can be confident that “automatic imitation” effects are not due to automatic emulation.

Imitation Versus Spatial Compatibility

There is a substantially greater risk of confusing automatic imitation with spatial compatibility (e.g., Aicken, Wilson, Williams, & Mon-Williams, 2007; Bertenthal, Longo, & Kosobud, 2006; Jansson, Wilson, Williams, & Mon-Williams, 2007). In

¹ The topographic features of an action are a subset of its spatial features. Therefore, it is potentially misleading to contrast automatic imitation, which depends on the topographic features of action, with “spatial compatibility.” However, the term “spatial compatibility” is used here to denote an alternative to automatic imitation because this usage is conventional in the literature reviewed.

many automatic imitation experiments, stimulus movements have been presented in the same left-right or up-down spatial alignment as that in which the participants' response movements were made. Therefore, it is possible that a tendency to respond in the same relative position as the stimulus (spatial compatibility) has been mistaken for a tendency to produce a topographically similar response, that is, to make "movement compatible" (Brass, Bekkering, & Prinz, 2001) or "imitatively compatible" (Catmur & Heyes, in press) responses, or to respond with the same "configural body movement" (Press et al., 2008). For example, in one of the original studies of automatic imitation (Stürmer et al., 2000), participants observed and executed hand movements in which the opening gesture consisted of a predominantly upward movement, and the closing gesture consisted of a predominantly downward movement. Consequently, faster responding in compatible than incompatible trials could have been due to an impulse to open one's hand when observing hand opening (automatic imitation) or to respond upward when observing an upward stimulus (spatial compatibility).

Eleven pairs of action types have been used in experiments on automatic imitation. In seven of these cases, the majority, there is clear evidence that automatic imitation effects are not due solely to spatial compatibility: power/precision grip (Chong, Cunningham, Williams, & Mattingley, 2009), index finger lifting/tapping (Brass, Bekkering, & Prinz, 2001), index/middle finger movement (Bertenthal et al., 2006), index/little finger abduction (Catmur & Heyes, in press), hand opening/closing (Heyes et al., 2005; Press et al., 2008), mouth opening/closing (Leighton & Heyes, 2010), and hand/mouth movement (Leighton & Heyes, 2010). These studies report automatic imitation effects when left-right, up-down, and/or orthogonal spatial compatibility have been controlled. In one of the 11 cases, variables relevant to spatial compatibility have been examined, but the results are not yet conclusive: horizontal/vertical arm movement (Gowen et al., 2008; Kilner et al., 2007, 2003; Stanley et al., 2007). In three cases, the role of spatial compatibility in generating the observed effects has not been investigated systematically: left/right grip orientation (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero et al., 1998, 1996), horizontal/vertical grip orientation (Vogt, Taylor, & Hopkins, 2003), and hand/foot movement (Bach et al., 2007; Gillmeister et al., 2008; Wiggett, Hudson, Tipper, & Downing, in press). Studies in which automatic imitation has been isolated from spatial compatibility ("finger movements" and "hand/mouth, opening/closing"), and research relating to the still ambiguous case ("arm movements"), are reviewed below.

Finger movements. A recent study by Chong et al. (2009, Experiment 1) showed that automatic imitation of *power/precision grip* is not due to left-right spatial compatibility. This study used a go-no go procedure in which participants were informed at the beginning of the trial by a numerical stimulus whether they were to perform a power or precision grip with their right hand in the event of a go trial. After a variable interval, an image of a hand was presented, which indicated whether the specified response should or should not be made, and, in the former case, acted as a cue for its immediate execution. The hand image showed a right or a left hand from a third person perspective, in a posture typical of a power or precision grip. Responding was faster when the go stimulus was response-compatible (e.g., power grip response to a power grip stimulus) than when it was response-incompatible (e.g.,

power grip response to a precision grip stimulus), and this automatic imitation effect was no greater when imitatively compatible responses were also spatially compatible (left hand stimuli) than when they were spatially incompatible (right hand stimuli).

The primary evidence that automatic imitation of *index finger lifting/tapping* is not reducible to up-down spatial compatibility came from an early, elegant experiment in which the action stimuli were inverted or "flipped" (Brass, Bekkering, & Prinz, 2001, Experiment 3). Participants showed an automatic imitation effect (e.g., faster tapping responses to the onset of tapping than of lifting stimuli), in spite of the fact that tapping responses (downward motion) were spatially incompatible with tapping stimuli (upward motion) and were spatially compatible with lifting stimuli (downward motion).

Later, Bertenthal et al. (2006, Experiment 3b) controlled for left-right spatial compatibility in the *index/middle finger* paradigm by requiring participants to make right hand responses to both left and right stimulus hands. They found an automatic imitation effect (e.g., faster index finger responses to the onset of index than middle finger movements) when, by instruction, both imitatively compatible and imitative incompatible responses occurred in the same left-right spatial position as their eliciting stimuli. The automatic imitation effect was small under these conditions, but this may have been due to the presentation of left and right hand stimuli in separate blocks, allowing the development of response strategies. When Catmur and Heyes (in press), examining *index and little finger abduction* movements, presented left and right hand stimulus trials in random order, they found substantial automatic imitation effects when the imitatively compatible responses were spatially compatible (e.g., right hand index response in the presence of a right hand index stimulus) and when they were spatially incompatible (e.g., right hand index response in the presence of a left hand index stimulus).

In addition to the findings reported above, Brass, Bekkering, and Prinz (2001) and Bertenthal et al. (2006) found evidence that when the index lift/tap and index/middle finger paradigms are used in the standard way—without flipping, or the presentation of both left and right stimulus hands—spatial compatibility may contribute to the magnitude of effects attributed to automatic imitation.

Hand/mouth, opening/closing. Studies examining opening and closing movements suggest that, even in their standard forms, these procedures isolate automatic imitation from spatial compatibility. In the case of the *hand opening/closing* paradigm, introduced by Stürmer et al. (2000), it is now standard to present the stimulus movements in a plane orthogonal to that of the response movements, thereby controlling for left-right and up-down spatial compatibility (Heyes et al., 2005; Wang, Newport, & Hamilton, in press). A study varying the anatomical identity of the stimulus hand, and response hemispace, has also confirmed that simple orthogonal spatial compatibility (e.g., a tendency to respond to up stimuli with right responses; Weeks & Proctor, 1990) and complex orthogonal spatial compatibility (e.g., a tendency to respond to up stimuli with right responses in right hemispace, and to down stimuli with right responses in left hemispace; Cho & Proctor, 2004) do not contribute to automatic imitation effects in the hand open/close procedure (Press et al., 2008).

A study by Leighton and Heyes (2010, Experiment 2) provided evidence that *mouth open/close* and *hand/mouth* compatibility effects are not due to left-right or up-down spatial compatibility.

For example, mouth opening responses were faster in the presence of mouth opening than of mouth closing stimuli, and this effect was not reduced when the mouth stimuli were rotated such that the lips moved in a horizontal rather than a vertical plane. Similarly, hand movements were faster in the presence of irrelevant hand movements than irrelevant mouth movements, and this effect was not reduced when the response hand was located directly in front of the mouth (not in a canonical position).

Arm movements. It is not yet clear to what extent the compatibility effects observed with horizontal/vertical arm movements are due to spatial, rather than topographical, relations between the stimuli and responses. Some studies suggest that compatibility effects can be obtained both when the movement stimulus is a human arm and when it is a dot; for example, under both of these conditions, vertical sinusoidal arm movements may be performed with more lateral error during observation of horizontal than vertical movements (Kilner et al., 2007; Stanley et al., 2007; but see also Gowen et al., 2008). Equivalence of this kind, between the effects of movement stimuli with animate and inanimate forms, has been taken to indicate that, in both cases, the effects are due to spatial compatibility (Jansson et al., 2007). This is not a valid inference, in general or in the particular case of horizontal/vertical arm movements. The inference is not generally valid because, even when they are of similar magnitude, compatibility effects involving animate and inanimate form stimuli could be based on different stimulus dimensions: left-right spatial properties of the inanimate stimuli, and topographical properties of the animate stimuli. In the case of horizontal/vertical arm movements, the inference is further obstructed by evidence that, for both arm and dot stimuli, constant velocity stimulus movements yield smaller effects than stimulus movements that decelerate as they approach their endpoints, that is, with “minimum jerk” velocity profiles (Chaminade, Franklin, Oztop, & Cheng, 2005; Kilner et al., 2007, 2003; but also see Stanley et al., 2007, Experiment 1). In these experiments, the purely spatial coordinates of the minimum jerk and constant velocity movements were identical; they were made between exactly the same up-down (vertical) and left-right (horizontal) endpoints. Therefore, this finding suggests that, at least when the observed movement has a minimum jerk profile, the interference effect is not due purely to spatial compatibility. Given that minimum jerk profiles are characteristic of biological motion, it also motivates the hypothesis that minimum jerk stimuli generate interference by virtue of mechanisms specific to the processing of biological motion.

However, there is another issue that currently makes it difficult to exclude the possibility that horizontal/vertical arm movement interference effects depend on spatial compatibility. Unlike the other effects providing putative examples of automatic imitation, those involving horizontal/vertical arm movements are asymmetric. Response movements always have a minimum jerk profile. Therefore, although some studies suggest that, for minimum jerk responses, observation of minimum jerk movement in the orthogonal plane generates more error than observation of constant velocity movement in the orthogonal plane, there is no evidence that the reverse is true for constant velocity responses. This asymmetry raises the question whether the effect of velocity profile is really a compatibility effect. It may depend on properties of the stimulus movements (not on the relationship between the stimuli and responses). For example, constant velocity movements may be

associated with smaller interference effects simply because, by virtue of their constancy, they are easier to ignore. Until this possibility is excluded, it will remain unclear whether horizontal/vertical arm movement interference effects are due to spatial compatibility or whether they derive from processes involved more specifically in the representation of observed and executed actions.

To conclude, it is not yet clear to what extent, if any, certain effects are due to spatial compatibility rather than automatic imitation. This uncertainty remains for two grip manipulations (left/right and horizontal/vertical), for hand/foot movement, and for horizontal/vertical arm movements. Given that left/right and horizontal/vertical grips are defined by their left-right and up-down spatial coordinates, it seems likely that spatial compatibility contributes to these effects. However, in the case of hand/foot movements, the finding that hand/mouth movement compatibility effects are not contaminated by up-down spatial compatibility (Leighton & Heyes, 2010) provides grounds for optimism that hand/foot effects will be found to be similarly “pure.”

For all of the other paradigms used to assess automatic imitation, there is evidence that the effects are not reducible to spatial compatibility. In some of these cases (index finger lifting/tapping, index/middle finger movement), the findings suggest that nonstandard controls may be needed to ensure that the RT (or error) difference between compatible and incompatible trials does not compound the effects of automatic imitation and spatial compatibility. In the remaining cases (precision/power grip, index/little finger abduction, hand opening/closing, mouth opening/closing, and hand/mouth movement), it appears that standard controls are sufficient to ensure that estimates of the magnitude of automatic imitation effects are not confounded by spatial compatibility.

Movements and Effectors

The research discussed above identifies a number of effects that are not due to automatic emulation or to spatial compatibility. These are all imitative effects in that they depend on topographical similarity—the degree to which the stimulus and response actions involve the same spatial relationships among parts of the body. However, these imitative effects are of at least two kinds: “movement compatibility” and “effector compatibility.” Movement compatibility effects depend on how parts of the body *move* relative to one another, whereas effector compatibility effects depend on how parts of the body are *located* relative to one another—on the anatomical identities of the stimulus and response effectors.

Movement compatibility effects include those observed using index finger lift/tap, hand open/close, and mouth open/close actions. For example, given that a compatibility effect has been reported with flipped stimuli depicting lifting and tapping movements (Brass, Bekkering, & Prinz, 2001), it is clear that this effect depends on the movement of the index finger relative to the rest of the model’s hand and not on the direction of movement relative to a substrate or other spatial coordinates. Similarly, the hand opening/closing compatibility effect depends on the movement of the fingers relative to one another and to the palm (Press et al., 2008), and the mouth opening/closing effect on the movement of the lips relative to one another and, possibly, to other facial features such as the nose (Leighton & Heyes, 2010). In contrast, it is likely that experiments involving index/middle finger lift, index/little finger

abduction, and hand/mouth actions provide evidence of effector compatibility. For example, the index/middle finger effect appears to depend on the anatomical identity (index or middle) of the finger that moves (not on the way in which the finger moves relative to the rest of the hand). Once up-down and left-right spatial compatibility has been controlled, the anatomical identity of a finger can be defined by its location relative to other parts of the hand, including the thumb. In the case of the “middle finger,” even the conventional name of the body part makes clear that its anatomical identity depends on its position relative to other digits.

Only one study has attempted explicitly to dissociate effector compatibility from movement compatibility (Leighton & Heyes, 2010). The results of each of the three experiments in this study indicate two effects: (a) effector compatibility—hand responses (open and close) were initiated faster during the observation of irrelevant hand movements (open and close) than during the observation of irrelevant mouth movements (open and close), and vice versa for the mouth responses—and (b) movement compatibility—opening responses (hand and mouth) were initiated faster during the observation of irrelevant opening movements (hand and mouth) than during the observation of irrelevant closing movements (hand and mouth), and vice versa for closing responses. These findings suggest that, regardless of the specific movement performed (e.g., opening or closing), there is a tendency for the observation of hand movement to facilitate hand rather than mouth responses, and a tendency for the observation of mouth movements to facilitate mouth rather than hand responses.

Supporting the suggestion that effector compatibility can be dissociated from movement compatibility, Bach et al. (2007) found a “body part priming” effect when the priming effector stimulus was not moving at all. In this study, colored imperative cues, or “targets,” were presented on static images of a whole human body. Foot responses were faster when the targets appeared at the model’s feet than when they appeared close to the model’s hands, and vice versa for hand responses. This result suggests that, in some automatic imitation paradigms, the movement of an effector may serve only to draw attention to the part of the body that is moving. In this case, the compatibility effect is due solely to the anatomical relationship between the attended body part and the response effector.

It is possible that the effects observed in experiments examining index/middle finger movements (Bertenthal et al., 2006; Brass et al., 2000; Longo & Bertenthal, 2009; Longo et al., 2008; Spengler et al., 2010) and index/little finger movements (Catmur & Heyes, in press; Catmur et al., 2007, 2009) are due to a combination of movement and effector compatibility or are due to effector compatibility entirely. Factorial experiments, crossing a movement variable with the effector variable (Leighton & Heyes, 2010), would indicate whether movement compatibility contributes to these effects.

Although they are distinct from movement compatibility effects, effector compatibility effects also depend on topographic relations. Therefore, although it is comparatively rare to describe as “imitation” use of the same body part as a model, effector compatibility effects, like movement compatibility effects, are closely related to canonical examples of imitation. Like overt behavioral imitation, they depend on topographical similarity between stimulus and response actions.

In conclusion, the studies reviewed in this section have established that automatic imitation is distinct from emulation—it is generated by body stimuli rather than object stimuli—and from spatial compatibility—it depends on topographic properties of body movements rather than their simple up-down, left-right, or orthogonal spatial features. Together, these findings indicate that automatic imitation, comprising both movement compatibility and effector compatibility effects, is indeed “imitation”—a covert form of imitation in which the observation of body movements activates motor representations of topographically similar body movements. Thus, these results suggest that the relationship between automatic imitation and overt behavioral imitation—imitation of the kind observed when people are instructed to imitate and in studies of motor mimicry—is similar to the relationship between silent reading and reading aloud. Neither automatic imitation nor silent reading is manifest in behavior; their occurrence is inferred on the basis of indirect measures such as response latency and error data. However, the evidence reviewed in this section suggests that, just as silent reading involves the same core cognitive processes as reading aloud, automatic imitation depends on the same core cognitive processes as overt behavioral imitation. Now, we turn to a further question: To what extent, and in what ways, are these processes “automatic”?

Is Automatic Imitation Really “Automatic”?

The automaticity of psychological processes has been judged against at least three criteria: interference, awareness, and intentionality (Neumann, 1984). The interference criterion implies that processes are automatic to the extent that they are immune to interference from, and do not interfere with, other processes. Given that most automatic imitation effects are, broadly speaking, interference effects—they consist in the modulation of task performance by irrelevant action cues—it is clear that automatic imitation is not thought to be automatic in this sense. The awareness criterion suggests that processes are automatic if they do not give rise to conscious awareness. This criterion has been applied in research on “unconscious” motor mimicry as a means of establishing whether motor mimicry is intended (e.g., Chartrand & Van Baaren, 2009; Hassin, Uleman, & Bargh, 2005), but, to date, it has not been used in research on automatic imitation. The intentionality criterion implies that a process is automatic to the extent that it is independent of the actor’s intentions. This is the defining sense of automaticity in the case of “automatic imitation.”

The question whether automatic imitation depends on the actor’s intentions is approached first in a common sense way—drawing on our pretheoretic understanding of what is meant by “intention”—and then with reference to “dual-route models” (Kornblum, Hasbroucq, & Osman, 1990), which currently provide the dominant theoretical account of SRC effects.

Common Sense Approach

From a common sense perspective, several factors make it unlikely that participants in automatic imitation experiments intend their behavior to be influenced by the task-irrelevant action stimuli. First, and by definition, they are not instructed to respond to these stimuli. For example, in the hand opening/closing paradigm, participants are instructed to respond to the color of the hand

stimulus (Stürmer et al., 2000) or to the onset of any movement of the hand stimulus (e.g., Heyes et al., 2005). They are not instructed to respond to the stimulus dimension that generates the RT difference between compatible and incompatible trials, that is, to the opening or closing properties of the hand stimuli.

In several experiments, participants have been required to imitate in some blocks (i.e., to match topographical features of the action stimuli) and to respond to nontopographical features in other blocks (Bertenthal et al., 2006; Brass et al., 2000). For these experiments, it could be argued that compatibility effects occur in blocks of the latter kind because participants have confused the instructions given at the beginning of each block type. For example, they may have intended to lift their index fingers when they saw index finger lifting, because that is what they had been required to do in previous blocks. On this view, automatic imitation effects are due to the right intention being implemented at the wrong time. There is independent evidence that this kind of confusion can modulate performance in SRC and task-switching paradigms (Hedge & Marsh, 1975; Hommel, 2000; Ocampo & Kritikos, 2010; van Schie et al., 2008), but it cannot account for the vast majority of automatic imitation effects. In most cases, automatic imitation occurs when the task instructions make no reference to imitation and when participants are not asked to imitate at any point in the experiment.

Second, automatic imitation effects can occur when participants do not intend to direct spatial attention to the action stimuli that generate the effects. Automatic imitation effects have been observed not only when the task-irrelevant stimuli are part of the same object as the task-relevant stimuli but also when they are spatially distinct. Under these conditions, to obey task instructions, the participant does not need to attend to the objects that generate automatic imitation effects, and in some experiments, they have been told explicitly that these objects are irrelevant and can be ignored (Leighton & Heyes, 2010). For example, imitative compatibility effects have been observed in index/middle finger (Brass et al., 2000) and index/little finger (Catmur & Heyes, *in press*) paradigms when the imperative cues were located between the fingers. Providing more extreme examples of spatial separation, Leighton and Heyes (2010) observed hand opening/closing, mouth opening/closing, and hand/mouth automatic imitation effects when imperative cues were presented at fixation and irrelevant action images appeared in the periphery of the visual field.

Third, automatic imitation occurs under conditions where it interferes with performance, preventing participants from doing what they have been asked to do—to respond swiftly and accurately to the task-relevant cue. Many automatic imitation effects consist of an RT or error difference between imitatively compatible and imitatively incompatible trials. In principle, these differences could be due entirely to facilitation of responding in imitatively compatible trials. However, evidence that they are due, at least in part, to interference rather than facilitation comes from studies showing that responding is slower in imitatively incompatible trials than in baseline trials where the task-relevant cue is presented in the absence of a task-irrelevant movement stimulus (Bertenthal et al., 2006; Brass et al., 2000; Gillmeister et al., 2008). It is unlikely that participants activate intentionally a process that interferes with their performance. Therefore, these data suggest that the process producing automatic imitation is not initiated intentionally.

Finally, automatic imitation occurs when participants are not ready to perform a response of the incompatible kind. At the beginning of each trial in choice RT paradigms, the participant is ready—he or she has an active intention—to make each of the responses that could be cued in that trial. However, like spatial compatibility effects (Hommel, 1996), automatic imitation effects occur not only in choice RT tasks but also in simple RT paradigms, where participants are making the same, prespecified response in each successive trial. Thus, for example, it appears that the sight of a closing hand can activate a representation of hand closing even when this action is not part of the currently activated response set.

Thus, there is evidence that automatic imitation effects occur when (a) participants have not been instructed to respond to the body movement stimuli that generate the effects, (b) they are not required by task instructions to attend to the locations at which those stimuli appear, (c) their responses to the irrelevant stimuli interfere with performance, and (d) the interfering response is not part of the currently active response set. At a common sense level, these features suggest that automatic imitation is minimally dependent on the actor's intentions.

Dual-Route Models

Over the last 25 years, the most influential theoretical accounts of SRC effects have assumed that responses can be activated via two distinct routes: an intentional (or “conditional” or “controlled”) route and an automatic (or “unconditional”) route (Proctor & Vu, 2006). Given that automatic imitation is a type of SRC effect, these dual-route models provide a rigorous theoretical context in which to examine the putative automaticity of automatic imitation.

Dual-route models assume that, once it has been identified through perceptual analysis, the task-relevant stimulus or stimulus dimension activates the correct response via the intentional route. This route is often modeled as a short-term S-R connection—an excitatory link between a stimulus (or “sensory”) representation (or “code”) and a response (or “motor”) representation (or “code”), which is established on the basis of task instructions and is held in short-term memory for the duration of the task (Barber & O’Leary, 1997; Zorzi & Umiltà, 1995). In addition, the task-irrelevant stimulus or stimulus dimension activates a similar or “corresponding” response via the automatic route. This route is typically modeled as a long-term S-R connection—an excitatory link between a stimulus representation and a response representation, which is either genetically prespecified or a product of learning and is held in long-term memory. If the intentional and automatic routes activate the same response representation (compatible trials), the correct response is executed rapidly. However, if the two routes activate different response representations (incompatible trials), the incorrect response, activated via the automatic route, must be inhibited in favor of the correct response. This takes extra time, and therefore responding is slower in incompatible trials.

This dual-route framework may be applicable to automatic imitation (see Figure 1). For example, instructing participants to respond to a blue stimulus with hand opening, and to a red stimulus with hand closing, results in the establishment of two short-term S-R associations, one connecting a blue code (X in Figure 1) with hand opening (Motor A) and the other connecting a red code (Y) with hand closing (Motor B; intentional route). By hypothesis,

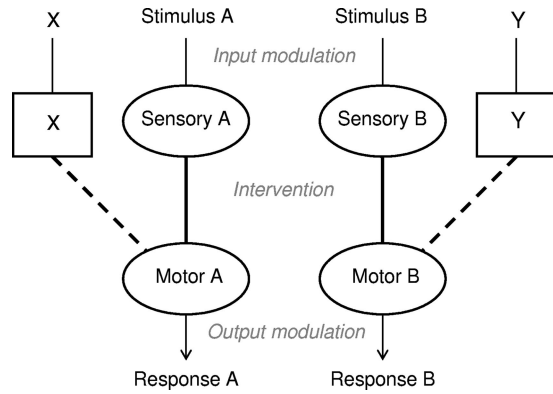


Figure 1. The dual-route model of stimulus-response compatibility applied to automatic imitation. The solid lines connecting sensory and motor representations of Action A (e.g., hand opening) and Action B (e.g., hand closing) indicate long-term associations and constitute the automatic route. The dashed lines connecting sensory representations of X (e.g., blue) and Y (e.g., red) to motor representations of A and B indicate short-term associations established by task instructions and constitute the intentional route. Input modulation impacts the activation of sensory representations. Output modulation influences the extent to which motor activation gains control of behavior. If it occurs, intervention affects the process propagating activation from sensory to motor representations via the “automatic” route.

participants bring with them to the experiment two long-term S-R associations, one connecting a hand opening stimulus representation (Sensory A) with a topographically similar hand opening response representation (Motor A), and the other connecting a hand closing stimulus representation (Sensory B) with a topographically similar hand closing response representation (Motor B; automatic route). When a blue stimulus is presented with an image of an open hand (compatible trial), the correct response—hand opening—is activated via both the intentional and the automatic routes, and therefore responses are initiated rapidly. When a blue stimulus is presented with an image of a closed hand (incompatible trial), the correct response—hand opening—is activated via the intentional route, but the incorrect response—hand closing—is activated via the automatic route. Therefore, the incorrect response must be inhibited, and responses are initiated relatively slowly.

Thus, in the case of automatic imitation, the process that may or may not be automatic is that which enables observation of the task-irrelevant action stimuli to activate motor representations coding topographically similar responses. Within the dual-route framework, this process is regarded as automatic if it is mediated by a long-term excitatory link between sensory and motor representations of the same action. If automatic imitation is produced by an S-R link of this kind, one would expect it to be subject to certain kinds of intentional modulation and not to others (Heyes & Bird, 2007). Specifically, it should be possible for the actor’s intentions to modulate the magnitude of automatic imitation effects by influencing the processing of the action stimulus (“input modulation”) and by influencing the extent to which motor activation of a corresponding response is inhibited or allowed to influence overt responding (“output modulation”). However, it should not be possible for the actor’s intentions to “intervene,” that is, to modulate an automatic imitation effect by changing the extent to which

activation of the stimulus representation results in activation of the response representation. In other words, one would not expect intentional factors to change the strength of a long-term S-R link.

These predictions—expressed in terms of a tripartite distinction between input modulation, output modulation, and intervention—are consistent not only with the basic principles of dual-route models but also with their more specific assumptions about automaticity. For example, presenting the influential “dimensional overlap” dual-route model, Kornblum et al. (1990) suggested that an automatic process is

normally triggered without the actor’s intending to do so and without attention directed at its object, but is facilitated by having attention focused on it [input modulation]. According to this view, an automatic process could under some conditions be attenuated or enhanced [input and/or output modulation]. However, under no conditions could it be ignored or bypassed [intervention]. (p. 261)

The first of the three sections below reviews evidence that automatic imitation is subject to input modulation. This evidence currently consists of studies showing that intentionally mediated changes in attention can influence automatic imitation. The second section describes studies that have been interpreted as demonstrating output modulation. These suggest that social cognitive variables can influence automatic imitation by inhibiting motor activation after that link has operated (not by changing the properties of a long-term S-R link). The third section discusses studies of “conceptual compatibility” and “counter-imitative task set” that have been interpreted as evidence of intervention—evidence that intentional variables can modulate automatic imitation by changing the process that translates activation of a stimulus representation into activation of a response representation. If this interpretation is correct, there would be reason to doubt that “automatic imitation” is automatic.

Input modulation. Automatic imitation occurs when task-irrelevant movement stimuli are presented in the periphery of the visual field (Leighton & Heyes, 2010; see “Common Sense Approach”). This suggests that automatic imitation does not require that participants intentionally direct their attention to the stimuli that generate the effects. However, there is evidence that intentionally mediated changes in spatial attention and feature selection can influence the magnitude of automatic imitation effects.

Several studies of “animacy”—comparing the magnitude of automatic imitation effects generated by natural human movements and by “artificial,” “impossible,” or “robotic” movements—have pointed to this conclusion (Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Longo et al., 2008). For example, Longo et al. (2008) asked participants to respond to the left-right spatial position of index and middle finger tapping movements that were either possible (normal joint movements) or impossible (abnormal joint movements). When the task instructions made no reference to the possibility variable, the automatic imitation effect (e.g., faster index finger responses to index than to middle finger stimuli) was of equal magnitude in the possible and impossible conditions. However, in another experiment, where participants were told that they would see both natural and impossible movements, an automatic imitation effect occurred only in the blocks where possible actions were presented. Similarly, when Longo and Bertenthal (2009) presented each participant with both photographic and computer-generated hand stimuli and mentioned that some of the

stimuli would be computer-generated, the index/middle finger compatibility effect for computer-generated stimuli was smaller than for photographic stimuli. It was also smaller than the automatic imitation effect observed in another group of participants who saw only computer-generated stimuli and were not told about their origins before the experiment began.

These results were interpreted, plausibly, as effects of instructions on attention (Longo & Bertenthal, 2009; Longo et al., 2008). When the instructions did not mention the impossible or computer-generated character of the stimuli, participants attended to the endpoint of each movement, and both possible/photographic and impossible/computer-generated movements produced an effector compatibility effect (see the Movements and Effectors section). When the instructions alluded to the possibility variable, participants shifted their attention from movement endpoints to movement kinematics, and the impossible/computer-generated stimuli failed to produce a substantial movement compatibility effect because their kinematics were unfamiliar, or dissimilar, to those of the tapping responses (see the Why Do We Imitate Automatically? section).

Other animacy studies have examined the magnitude of automatic imitation effects produced by natural human movement stimuli as a function of participants' beliefs about the origins of those stimuli. For example, before testing participants with index and middle finger movements of a gloved human hand, Liepelt and Brass (2010) told one group of participants, with an illustration, that the movements had been generated by a wooden hand. This group showed a smaller automatic imitation effect than the group that believed they were observing human movements. As the authors acknowledged (Liepelt & Brass, 2010), like the animacy effects reported by Longo et al. (2008; Longo & Bertenthal, 2009), this result could have been due to closer attention to movement kinematics in the wooden hand group. If the index/middle finger automatic imitation effect depends primarily on effector, rather than movement, compatibility, perceptual selection of kinematics would be expected to erode the magnitude of the effect.

In another study examining beliefs about action stimuli, Liepelt et al. (2008, Experiment 2) found a larger index/middle automatic imitation effect when fractional finger movements were presented inside, rather than alongside, metal clamps. This may indicate that, because of enhanced attention or via some other route, automatic imitation is modulated by beliefs about the effort involved in making stimulus movements. However, these results must be interpreted with caution because the study used a first person variant of the index/middle finger paradigm that has not yet been shown to isolate automatic imitation from spatial compatibility.

In experiments similar to those of Longo et al. (2008; Longo & Bertenthal, 2009) and Liepelt et al. (2008; Liepelt & Brass, 2010), Press, Gillmeister, and Heyes (2006) found that hand open/close compatibility effects were not modulated by instructions concerning the human or robotic origins of the movement stimuli or by whether the stimulus movements were performed by a hand with a natural human wrist or a robotic wire wrist. These negative results are unlikely to have been due to test insensitivity because the same paradigm has shown that automatic imitation can be modulated by intrinsic properties of the movement stimuli (Press et al., 2005, 2006). Therefore, they imply that automatic imitation of hand opening/closing, assessed in a simple RT task, is less

susceptible to the influence of attention than automatic imitation of index/little finger movements, assessed in a choice RT task.

More direct evidence that automatic imitation can be modulated by attention comes from a study that varied the location of the imperative cue relative to the action stimuli eliciting the compatibility effect (Bach et al., 2007, Experiment 1). Participants were instructed to respond with their foot or their hand, depending on the color of a dot presented near the head, hand, or foot in whole body images depicting hand or foot action. There was an automatic imitation effect (e.g., faster foot responses when the actor was performing a foot than a hand action) when the imperative stimuli appeared close to the acting effector but not when the dots appeared close to the actor's head.

In another study designed explicitly to examine the effect of attention on automatic imitation, Chong et al. (2009, Experiment 2) presented go–no go stimuli consisting of a red or blue diamond superimposed on a hand in a power or precision grip posture. There was an automatic imitation effect (e.g., faster execution of power grip with a power than a precision grip cue) when participants were instructed to use stimulus grip as the go–no go signal but not when they were instructed to use color as the go/no go signal. Similar results were obtained in a follow-up experiment where participants were instructed to use either the laterality (left or right) or the grip posture (power or precision) of a hand stimulus as go–no go stimuli (Chong et al., 2009, Experiment 3). Again, there was an automatic imitation effect when grip, but not when laterality, was the go–no go signal.

These results could be due to attentional modulation of automatic imitation, but they could also be due to RT differences between conditions. Responding in the “attend grip” condition was significantly slower than in the “attend color” condition (Chong et al., 2009, Experiment 2) and was significantly faster than in the “attend laterality” condition (Experiment 3). Therefore, it is possible that an automatic imitation effect was not detected in the “attend color” condition because responses were initiated before perceptual processing of grip type was sufficiently advanced to activate topographical similar motor representations, and that it was not detected in the “attend laterality” condition because the motor activation generated by grip type had decayed before responses were initiated. A number of studies examining the magnitude of automatic imitation effects across the RT distribution have shown that they tend to increase and then to decline with response latency (e.g., Brass, Bekkering, & Prinz, 2001; Catmur & Heyes, *in press*).

Although the results of the study by Chong et al. (2009) are not conclusive, there is both direct (Bach et al., 2007) and indirect (Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Longo et al., 2008) evidence that the magnitude of automatic imitation effects can be modulated by attention. Judged against some earlier, general accounts of automaticity (Chong & Mattingley, 2009; Posner, 1978; Shiffrin & Schneider, 1977), this evidence would count against the automaticity of automatic imitation. However, it is consistent with the automaticity postulated by more recent theories concerned specifically with the processes mediating SRC effects. These dual-route models acknowledge that an automatic process can be “facilitated by having attention focused on it[s object]” (Kornblum et al., 1990, p. 261)—that is, that it is subject to input modulation.

Output modulation. Research relevant to output modulation has been dominated by studies showing, through a variety of methods, that the magnitude of automatic imitation effects can be influenced by social cognitive processes. For example, Spengler et al. (2010) found that the index/middle finger automatic imitation effect was attenuated when “self-focus” was encouraged by allowing participants to view their own body in a mirror during testing or by requiring them to make evaluative, self-referential judgments between trials in the compatibility task. Similarly, Leighton et al. (2010; see also J. Cook & Bird, 2010b) tested participants in the hand open/close paradigm immediately after they had completed a scrambled sentence task. The automatic imitation effect was attenuated if the sentence task included antisocial words (e.g., rebel, independent, disagreeable, alone) and was enhanced if it included prosocial words (e.g., affiliate, friend, cooperate, together) relative to a condition in which the sentence task included only neutral words. Also, using the hand open/close procedure, Wang et al. (in press) found a larger automatic imitation effect when the movement stimulus was preceded by the actor making direct eye-contact with the participant than when it was preceded by averted gaze or by a centrally located flash of light.

These findings, from behavioral studies involving neurologically intact participants, support those of previous research involving functional imaging and patients with brain lesions. The imaging studies have shown consistently that two cortical areas associated with social cognitive functions, the anterior fronto-median cortex (aFMC) and the temporo-parietal junction (TPJ), are more active during incompatible than during compatible trials in the index lift/tap (Brass, Zysset, & von Cramon, 2001) and index/middle finger (Brass et al., 2005; Spengler, von Cramon, & Brass, 2010) automatic imitation paradigms. The neuropsychological studies have indicated that, in patients with frontal lesions and in controls, the magnitude of the index/middle finger automatic imitation effect is correlated with performance on an advanced theory of mind task and that in patients with TPJ lesions, it is correlated with indices of empathy, visual perspective-taking, and theory of mind (Spengler et al., 2010). In all cases, a larger automatic imitation effect predicted weaker performance on measures of social cognitive functioning.

Studies involving participants with ASC also suggest that social cognitive processes can modulate automatic imitation. Compared with controls, adults with ASC, who are known to have impairments in social cognitive functioning, show an enhanced automatic imitation effect in the hand open/close procedure (Bird et al., 2007), and in the index/middle finger procedure, the magnitude of their automatic imitation effects is not influenced by prosocial and antisocial priming using a scrambled sentence task (J. Cook & Bird, 2010a). Similarly, testing typically developing adults, Bach and Tipper (2007) found a correlation between Autism-Spectrum Quotient scores and the extent to which completion of a hand/foot automatic imitation procedure influenced participants’ judgments about the personality characteristics of the actors observed in the course of the procedure. For example, participants with high scores were more inclined to judge as “sporty” an actor who had been observed kicking a ball, rather than typing on a keyboard, when foot responses were made.

These findings have been interpreted as examples of output modulation, suggesting that social cognitive processes modulate the magnitude of automatic imitation effects by influencing the

extent to which corresponding motor activation is inhibited or allowed to influence overt behavioral performance (Bien, Roebroek, Goebel, & Sack, 2009; Brass, Ruby, & Spengler, 2009). More specifically, Brass et al. (2009) have proposed that two kinds of social cognitive function are involved in the modulation of automatic imitation. The first, associated with the TPJ, makes “agency” judgments; it classifies an observed body movement as either self-generated or other-generated. The second, associated with the aFMC, “is required to enforce one’s own motor intention against the externally triggered response tendency” (Brass et al., 2009, p. 2362). In other words, the aFMC mediates intentional processes that oppose the behavioral expression of motor activation generated automatically by perceptual processing of body movement. Factors influencing the efficiency of either or both functions—durably, as in the cases of brain injury and ASC, or transiently, via self-focus and social priming procedures—could have an impact on the magnitude of automatic imitation effects. For example, weak enforcement of the participant’s own intentions (based on task instructions) could be a direct effect of brain injury or social priming, or secondary to a reduction in the efficiency with which body movement stimuli are classified as other-generated rather than self-generated. In either case, weak enforcement of a participant’s own intentions would be expected to result in faster responding in imitatively compatible trials and/or slower responding in imitatively incompatible trials, because it would leave automatically activated motor representations relatively unopposed in gaining control of behavior.

The interaction between automatic imitation and (other) social cognitive functions is an exciting frontier in social cognitive neuroscience. There is much still to be learned, but, at present, research in this area suggests that higher social cognitive functions modulate automatic imitation, not by changing the process that normally generates corresponding motor activation but by regulating the behavioral output from this process. In other words, intention-related social cognitive processes appear to contribute to output modulation rather than intervention. Therefore, the studies reviewed in this section do not challenge the view that automatic imitation is “automatic” in the same sense as other SRC phenomena.

Intervention. Studies of conceptual compatibility and counter-imitative task set have been interpreted as evidence of intervention—that intentional variables can modulate automatic imitation, not only at input and output but also by changing the process that translates activation of a stimulus representation into activation of a response representation. If this is correct, it is unlikely that the translation process is mediated by a long-term S-R link and, therefore, that “automatic imitation” is automatic in the sense specified by dual-route models of SRC.

Jansson et al. (2007) have suggested that automatic imitation effects are either reducible to spatial compatibility (see the Spatial Compatibility section) or are due to conceptual compatibility. For example, the sight of hand opening may activate a verbal or semantic representation of “opening” (conceptual compatibility) rather than a motor representation of hand opening, that is, a specific, topographically similar response (imitative compatibility). In this case, the process producing “automatic” imitation effects would be mediated by higher order representations, and therefore it would be likely that higher order processes could intervene to prevent it from running its course.

In support of their proposal, Jansson et al. (2007, Experiment 2) showed that a compatibility effect could be obtained with hand opening/closing responses, not only when the stimuli depicted opening and closing hand actions but also when they consisted of two dots moving apart (opening) or together (closing). However, this result is ambiguous. It could be that the hand and dot compatibility effects were mediated by the same, conceptual process, but it is at least equally plausible that the dot effect was mediated by a conceptual process (or by orthogonal spatial compatibility; Press et al., 2008), whereas the hand effect was due to direct activation of motor responses by action stimuli.

An experiment by Leighton and Heyes (2010) provided a stronger test of the conceptual compatibility hypothesis. If the sight of hand opening activates an abstract verbal or semantic representation of “opening,” rather than a specific motor representation of hand opening, one would expect hand opening stimuli to be equally effective in priming hand opening and mouth opening responses. However, the results reported by Leighton and Heyes (Experiment 3) were contrary to this prediction. In a procedure where color stimuli cued one of four responses in each trial—hand open, hand close, mouth open, mouth close—and the imperative cue was accompanied by an irrelevant stimulus depicting one of the same four actions, the open/close compatibility effect was significantly greater when the stimulus effector was response-compatible than when it was response-incompatible. For example, open mouth responses were faster in the presence of open hand than of close hand stimuli, but the effect of the irrelevant hand stimuli was greater when participants were making open hand, than open mouth, responses. This pattern of results suggests that, rather than being conceptually mediated, the hand open/close compatibility effect is due directly to activation by movement observation of motor representations coding topographically similar responses.

In another study that has been interpreted as providing evidence of intervention, van Schie et al. (2008) showed that an automatic imitation effect can be reversed when trials in which the action cue is task-irrelevant are embedded in a counter-imitation task (for similar effects, see Heyes & Ray, 2004; Ocampo & Kritikos, 2010). In each trial in these experiments, participants saw an actor grasping the base of an object with a power grip, or the upper part of the object using a precision grip. In imitation blocks, they were asked to do the same as the actor (e.g., to respond to a power grip using a power grip), and in counter-imitation blocks, they were instructed to perform the opposite action (e.g., to respond to a power grip using a precision grip). The findings of interest were from probe trials presented in each of these block types. In probe trials, a component of the stimulus video (hand, object, or table) was colored green, indicating that the participant should make a prespecified response—for example, use a power grip regardless of the grip type applied by the model. In imitation blocks, probe trial responding was faster when the action stimulus was compatible with the prespecified response, but in counter-imitation blocks, probe trial responding was slower when the action stimulus was compatible with the prespecified response.

This striking reversal effect has been taken to indicate that higher order processes can intervene to determine whether perceptual analysis of action stimuli results in the activation of topographical similar or topographically dissimilar motor representations. However, the reversal effect is formally identical to the

“Hedge and Marsh effect” (Hedge & Marsh, 1975), which can be explained in terms of output modulation (De Jong, Liang, & Lauber, 1994). Instead of instructing participants to make grip responses to grip stimuli, Hedge and Marsh (1975) asked them to respond to red and green lights, appearing at an up or down location, by depressing red and green keys, which were also located at an up or down position on the response apparatus. In the congruent mapping condition (equivalent to the imitation condition in the experiments by van Schie et al., 2008), responses to the red light were made with the red key, and responses to the green light were made with the green key. In the incongruent mapping condition (equivalent to the counter-imitation condition), these S-R mappings were reversed. Hedge and Marsh found a typical spatial compatibility effect in the congruent mapping condition (a “Simon effect”; e.g., when the red key was above the green key, responses to a red light were faster when the red light appeared at the top, rather than the bottom, of the display). However, they found a reversed spatial compatibility effect in the incongruent mapping condition (e.g., when the red key was above the green key, responses to a red light were slower when the red light appeared at the top, rather than the bottom, of the display).

De Jong et al. (1994) provided a dual-route, “logical recoding” explanation for the Hedge and Marsh effect. This account assumes that incongruent mapping instructions are logically recoded, or overgeneralized, from the task-relevant (color) to the task-irrelevant (location) stimulus dimension. Consequently, the intentional route includes response rules, or short-term S-R links, connecting spatially incompatible stimuli and responses. These compete with the long-term S-R links that connect spatially compatible stimuli and responses and constitute the automatic route. Unless responses are made very fast, when automatic activation is strong, performance is dominated by the short-term, intentional links that promote spatially incompatible responding, and a reversal of the usual spatial compatibility effect is observed. Given the formal resemblance between the Hedge and Marsh effect and the reversed automatic imitation effect reported by van Schie et al. (2008), it is plausible that the latter is also due to the kind of output modulation process described by De Jong et al. That is, in counter-imitation blocks, intentional processes may have overwhelmed automatic activation in a competition for control of behavior. If so, the reversed automatic imitation effect is not an example of intervention; it does not show that intentional processes can change the long-term S-R links that promote topographically similar responses to task-irrelevant action stimuli.

Thus, research on conceptual compatibility and the influence of a counter-imitative task set does not currently provide compelling evidence that higher order cognitive processes can intervene in the process mediating automatic imitation. The conceptual compatibility hypothesis is inconsistent with the effector-dependence of automatic imitation, and the effect of counter-imitative task set could be due to logical recoding, that is, output modulation by intentional processes.

To conclude, the evidence reviewed in this section suggests that the process mediating automatic imitation is automatic, rather than intentional, when viewed both from a common sense perspective and in the context of dual-route models. In the latter case, there is evidence that automatic imitation can be modulated by intentionally driven changes in attention (“input modulation”) and by higher order social cognitive processes, which influence the degree

to which activation of a topographically similar response representation is inhibited or allowed to gain control of behavior (“output modulation”). However, at present, there is no unambiguous evidence that intentional processes can intervene between perceptual processing and motor activation to change the properties of the long-term S-R links that mediate automatic imitation (“intervention”). These features suggest that automatic imitation is “automatic,” not in the strong sense implied by some early theories of automaticity (Posner, 1978; Shiffrin & Schneider, 1977) but, according to dual-route models (Kornblum et al., 1990), in the same way as other processes that generate SRC effects.

Why Do We Imitate Automatically?

Why do we imitate automatically? By itself, the dual-route framework offers a simple, but not deep, answer to this question: because we have long-term associations linking sensory representations of topographical features of action with motor representations of the same or “corresponding” topographical features of action. This answer is helpful but not satisfying because it does not tell us *why* we have these long-term S-R associations. Why, for example, are sensory representations of hand opening connected with motor representations of hand opening rather than with motor representations of hand closing, or mouth opening, or pointing? This question, which is sometimes known as the “correspondence problem” (Brass & Heyes, 2005), has been answered in two ways. One answer assumes that all, or the majority, of the long-term associations mediating automatic imitation are learned; the other assumes that all or the majority are genetically prespecified or “innate.”

Origins of Long-Term Sensorimotor Connections

Two theoretical accounts have been applied specifically and in some detail to research on automatic imitation: ideomotor theory of action control (Massen & Prinz, 2009; Prinz, 2005) and the associative sequence learning (ASL) model of imitation (Catmur et al., 2009; Heyes, 2005). These accounts differ in emphasis. For example, ideomotor theory stresses that, once established, long-term associations between perceptual and motor representations constitute “common codes” or “shared representations” of action, whereas ASL focuses on the conditions and mechanisms necessary for the establishment of these long-term associations. However, both ideomotor theory and ASL are broadly consistent with dual-route models of SRC, and they both assume that the long-term S-R associations mediating automatic imitation are products of learning.

As far as I am aware, it has not been suggested explicitly that the long-term associations mediating automatic imitation are genetically prespecified. However, this is a coherent hypothesis and one that is consistent with theories that have been advanced in relation to phenomena that resemble, or are closely related to, automatic imitation. For example, some action researchers consider it to be an open question whether the long-term associations mediating spatial (rather than imitative) SRC effects are genetically prespecified or are due to learning (Hommel, 2000). Many developmental psychologists believe that human neonates can imitate a range of facial expressions, and that this is made possible by an innate “supramodal matching” mechanism (Meltzoff & Moore, 1997).

Similarly, comparative psychologists have suggested that nonhuman primates show “mimicry” (Tomasello, 1996) or “response facilitation” (Byrne & Russon, 1998)—immediate reproduction of observed behavior—because of simple, innate S-R links, and it is widely assumed that the perception–action matching properties of “mirror neurons” are present at, or shortly after, birth (Ferrari, Bonini, & Fogassi, 2009).

Until recently, a “poverty of the stimulus” argument motivated the hypothesis that imitative responses depend on inborn connections between sensory and motor representations of the same actions (Ray & Heyes, 2011). It is easy to think of circumstances in which developing infants have the opportunity to learn these connections for “visible” or “transparent” actions, such as hand movements, but harder to imagine conditions in which they could learn these connections for “invisible” or “opaque” actions (Heyes & Ray, 2000), such as facial expressions and whole body movements. For example, every time an infant watches his or her own hand performing a voluntary movement, s/he has the opportunity to strengthen a connection between the motor program that initiated the response (the “feel” of the action) and a sensory representation of its effects (the “look” of the action). A hand movement, such as splaying the fingers, looks much the same to me when I perform it and when I observe it performed by another person. Therefore, provided that the sensorimotor connections are bidirectional (activation of the sensory representation is propagated to the motor representation, and vice versa), learning through direct self-observation could be sufficient for imitation of transparent actions. Thus, when I observe you splaying your fingers, it looks similar to what I have seen whenever I have watched myself splaying my fingers and, therefore, activates the sensory representation of finger splaying that has been connected, through self-observation, to my motor representation of finger splaying.

However, learning based on direct self-observation is not sufficient to enable me to imitate opaque actions such as facial movements. What I see when I, for example, open my mouth, does not resemble what I see when I observe you opening your mouth. Therefore, any sensorimotor connections established during visual monitoring of my own mouth movement will not be activated when I observe another person moving their mouth. Thus, it is not obvious how infants would learn sensorimotor connections of the kind necessary for imitation of opaque actions, and therefore a “poverty of the stimulus” argument has encouraged the view that the connections necessary for imitation of both opaque and transparent actions are genetically prespecified.

Ray and Heyes (2011) recently reviewed evidence that infants and children learn connections between sensory and motor representations of the same actions, not only via direct self-observation but also in the context of a variety of social interactions. These included mirror self-observation, acquired equivalence experience, synchronous activities of the kind involved in sports and dance training, and, most importantly, being imitated by adults. For example, pointing out that being imitated by adults gives children the opportunity to see the effects of their actions as those effects are viewed by others (i.e., to form sensorimotor connections of a kind that would be activated by viewing another’s action), Ray and Heyes highlighted evidence that imitation of infants by adults occurs up to once every minute during face-to-face interactions in the first two years of life (Pawlby, 2007). Research of this kind makes it plausible that infants could learn sensorimotor connec-

tions of the sort required for imitation. However, it does not show specifically or in a direct way that automatic imitation depends on learned, rather than genetically prespecified, S-R connections. Direct tests of the learning hypothesis have been made using training methods.

Training Studies

Training studies have been based on a simple assumption: If automatic imitation effects are generated by long-term connections that result from learning, it should be possible to change those effects by further learning in an experimental environment. The first training study apparently confirmed this prediction by showing that an automatic imitation effect could be abolished by experience with imitatively incompatible S-R mappings (Heyes et al., 2005). Participants were tested for automatic imitation of hand opening/closing in a simple RT task 24 hr after performing 432 trials of a choice RT task in which they were required to respond to opening hand stimuli by closing their hands, and to closing hand stimuli by opening their hands (incompatible group), or vice versa (control group). A significant automatic imitation effect (e.g., faster hand opening responses in the presence of hand opening than of hand closing stimuli) was observed in the control group but not in the incompatible group. This difference is unlikely to have been due to the passage of time, to repeated exposure to the movement stimuli (sensory experience), or to repeated performance of the target actions (motor experience)—all of which were equated across groups. Rather, the absence of an automatic imitation effect in the incompatible training group appears to have been due to the fact that, during training, they observed the movement stimuli while performing noncorresponding actions (incompatible sensorimotor experience). This kind of sensorimotor experience could reduce automatic imitation by establishing inhibitory connections between sensory and corresponding motor representations of action (e.g., between sensory and motor representations of hand opening) and/or by establishing excitatory links between sensory and noncorresponding motor representations of action (e.g., between a sensory representation of hand opening and motor representation of hand closing).

In a follow-up study, R. Cook, Press, Dickinson, and Heyes (2010) examined more closely the type of training that reduces and abolishes automatic imitation. They found that incompatible sensorimotor experience had this effect only when there was a “contingency” or predictive relationship between hand movement stimuli and hand movement responses during training. For example, when this contingency was eroded, by including training trials in which responses occurred in the absence of movement stimuli, the effect of training was significantly reduced. Associative learning, of the kind that mediates instrumental conditioning in animals (Dickinson & Charnock, 1985) and humans (Elsner & Hommel, 2004; Shanks & Dickinson, 1991), is known to be sensitive to contingency. Therefore, this result is consistent with the hypothesis, central to the ASL model, that the long-term connections underlying automatic imitation are formed via species-general and domain-general processes of associative learning (Heyes, 2001; Heyes & Ray, 2000).

The reduction of automatic imitation by incompatible sensorimotor training has also been reported for hand/foot lifting responses (Gillmeister et al., 2008), indicating that this kind of

training is effective both when it is the movement properties (hand opening/closing) and the effector properties (hand/foot lifting) of the action stimuli that usually generate automatic activation (see the Movements and Effectors section). After training, the participants in the hand/foot lifting study were not only tested for automatic imitation but also were subjected to fMRI while observing and executing hand and foot movements (Catmur et al., 2008). In “mirror areas”—that is, regions of the premotor and parietal cortex that were activated by both action observation and action execution—the control participants showed hand dominance; blood oxygen level dependent (BOLD) responses were greater during observation of hand than of foot movements, consistent with the motor properties of these areas. In contrast, participants who had responded during training to the sight of hand movements using foot movements, and vice versa, showed foot dominance; BOLD responses were greater during observation of foot than hand movements, indicating that the observation of foot movements activated the motor representation of hand movements. Thus, this study links automatic imitation with the mirror neuron system, suggesting that both can be affected by incompatible sensorimotor experience (Catmur et al., 2009; Heyes, 2010).

A recent study by Wiggett et al. (in press) replicated the results reported by Gillmeister et al. (2008) using “response-effect” rather than “S-R” training. That is, rather than responding to hand stimuli with foot responses, and vice versa, the participants in the more recent study chose freely whether to make a hand or a foot action in any given training trial, and they saw an image of the alternative action on the computer screen immediately after action execution. This is an interesting result because both the ASL model and ideomotor theory assume that, in everyday life, long-term S-R connections are learned predominantly through experience in which movement stimuli follow, rather than precede, action execution.

In all of the foregoing studies, participants were given a modest amount of incompatible training, lasting up to 2 hr, which resulted in significant reduction or abolition of an automatic imitation effect. A study examining the effect of incompatible training on a mirror effect, rather than on automatic imitation, has provided evidence of reversal. For example, before training, observation of index finger abduction movements was associated with larger TMS-induced MEPs from an index finger muscle than observation of little finger movements, but after training, this pattern was reversed: For example, observation of little finger movements produced larger MEPs in the index finger muscle than observation of index finger movement (Catmur, Mars, Rushworth, & Heyes, in press; Catmur et al., 2007). Given that an automatic imitation effect has been observed with index/little finger abduction (Catmur & Heyes, in press), and that this effect is reduced when the mirror neuron system is disrupted by repetitive TMS (Catmur et al., 2009), this result suggests that more extended training than has been used to date may reverse automatic imitation, that is, yield an automatic “counter-imitation” effect.

A final training study has shown that, in addition to being reduced by incompatible sensorimotor training, automatic imitation can also be enhanced by compatible sensorimotor training. A number of studies have demonstrated animacy effects, that is, that natural human movements produce larger automatic imitation effects than artificial, impossible, or robotic movements (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Liepelt & Brass,

2010; Longo & Bertenthal, 2009; Longo et al., 2008). Animacy effects have been interpreted as evidence that automatic imitation is mediated by evolved mechanisms that are adapted for the processing of biological, rather than mechanical, motion. This would imply genetic prespecification of the long-term S-R connections that produce automatic imitation. Testing this hypothesis against the view that long-term S-R connections result from learning, Press, Gillmeister, and Heyes (2007) assessed automatic imitation of human and robotic hand opening/closing before and after compatible training with robotic movement stimuli. During training, participants were required to respond to robot hand opening by opening their hand, and to robot hand closing by closing their hand (compatible group), or vice versa (control group). Before training, both groups showed an animacy effect: The difference between RTs in compatible and incompatible trials was greater when the irrelevant movement stimuli were human rather than robotic. After training, the control group continued to show the same animacy effect, but in the group that had practiced compatible S-R mappings, the automatic imitation effect was as great for the robotic as for the human stimuli. These results are consistent with the view that animacy effects are due to learning. On this account, artificial, impossible or robotic movements normally elicit less automatic imitation than human movements because of “generalization decrement” (Pearce, 1987). Compared with human movements, artificial movements have fewer features in common with the sensory representations of action that have become connected, through lifelong learning, with motor representations of the same actions. Therefore, they activate these long-term connections less strongly and yield smaller automatic imitation effects.

In conclusion, both the ASL model and ideomotor theory assume that automatic imitation effects are generated by learned long-term connections between stimulus and response representations. This hypothesis has been supported by a number of training studies showing that incompatible sensorimotor experience can reduce or abolish automatic imitation of human movement stimuli, and that compatible sensorimotor experience can enhance automatic imitation of robotic movement stimuli. These training effects are likely to be due to learning rather than a transitory influence of experience on automatic imitation, because in most studies, they have been observed with an interval of at least 24 hr between training and testing. Although consistent with the view that automatic imitation depends on learning, to date the results of training studies do not exclude a role for genetic prespecification in establishing the long-term sensorimotor connections that generate automatic imitation. For example, it is possible that, owing to genetic factors, links between sensory and motor representations of the same action are easier to learn than links between sensory and motor representations of different actions. This possibility could be assessed by giving participants more extended incompatible sensorimotor training with antagonistic actions, for example, hand opening/closing. If more extensive training resulted, not only in the reduction or abolition but in the reversal of automatic imitation—in the formation of sensorimotor links between opposite actions—it would suggest that learning of these connections is not constrained or “prepared” by genetic factors. Genetically prespecified mechanisms can certainly be altered by events occurring within an individual’s lifetime. They can be damaged by physical trauma (Merzenich et al., 1984) and can be selectively enhanced by training and

experience (Elbert, Pantev, Wienbruch, & Rockstroh, 1995). However, such mechanisms are normally resistant to experience-dependent change that would substantially reduce their efficiency (abolition) or transform the way in which they function (reversal; Cosmides & Tooby, 1994; Heyes, 2010; Pinker, 1997).

Conclusions and Future Directions

The results of the research reviewed in this article imply that automatic imitation is an important new psychological phenomenon, comparable with the Stroop effect (Stroop, 1935) and the Simon effect (Simon, 1969). Like these other SRC effects, automatic imitation is “automatic” in the sense of being minimally dependent on the actor’s intentions. However, automatic imitation is distinctive in its dependence on fundamentally imitative relations—on the topographic similarity between action stimuli and action responses.

Research on mirror effects and motor mimicry suggests that these phenomena are relatively intention-independent and that they map action stimuli onto topographically similar responses. Therefore, the evidence—reviewed in this article—that “automatic imitation” is both automatic and imitation lends considerable weight to the hypotheses that automatic imitation is mediated by the mirror neuron system and that it constitutes a laboratory model of motor mimicry. This is important because it implies that automatic imitation can be used as an index of the functioning of the mirror neuron system and to examine in highly controlled experimental environments the mechanisms that enable social attitudes to modulate motor mimicry.

The human mirror neuron system has been studied using methods such as fMRI and TMS. The results of this review suggest that automatic imitation paradigms offer an accessible and cost-effective additional means of testing hypotheses about the functioning of the mirror neuron system. For example, a major outstanding question is whether the mirror neuron system plays a causal role in action understanding (Hickok & Hauser, 2010; Press, Heyes, & Kilner, in press). This question could be addressed by taking measures of both action recognition and automatic imitation before and after a period of disruptive incompatible sensorimotor training. If the mirror neuron system plays a functional role in action understanding, one would expect disruption of the mirror neuron system—indexed by a pre- to posttraining reduction in automatic imitation—to be proportional to any pre- to posttraining impairment in action recognition.

Previous research in naturalistic settings has shown that social attitudes modulate motor mimicry, but we do not yet know exactly how this relationship is mediated (Chartrand & Van Baaren, 2009). Do prosocial attitudes enhance mimicry directly or via their effects on attentional and affective variables? Do they promote the performance of exactly the same movements as the model or only the use of the same body parts? Are negative social attitudes associated with an absence of mimicry or with a systematic tendency to counter-imitate? Questions of this kind are crucial for understanding the psychological processes that mediate the relationship between social attitudes and motor mimicry, but they are very difficult to penetrate using naturalistic methods alone. The findings reviewed in this article suggest that automatic imitation paradigms can be used in some studies as a substitute for naturalistic,

frequency-based measures of motor mimicry. This would allow the nature and extent of participants' mimicry—indexed by the type and magnitude of automatic imitation effects—to be measured precisely under conditions where it is also possible to assess and control social, affective, and attentional variables.

Motor mimicry is an example of “simple” imitation, unintended copying of actions that are already part of the observer's behavioral repertoire. In more “complex” imitation, the observer unintentionally or deliberately acquires a novel sequence or pattern of body movements by copying a model (Heyes, in press). The research reviewed in this article suggests that automatic imitation is closely related to simple imitation; it is a partial or covert form of simple imitation in which action observation activates a corresponding motor representation but, because of inhibitory processes, seldom results in explicit performance of the observed action. The ASL model suggests that automatic imitation is also directly related to complex imitation. According to this model, the same long-term S-R links that generate automatic and simple imitation also solve the correspondence problem for complex imitation. Rather than symbolic or inferential processes, it is these links that make it possible to convert visual input from a novel sequence of behavior into corresponding motor output (Heyes, 2005). This hypothesis is consistent with the results of the “training studies” reviewed above and with evidence that complex imitation can be effector-dependent (Bird & Heyes, 2005). If the hypothesis is correct, automatic imitation not only provides a tool for research on the mirror neuron system and simple imitative phenomena, such as motor mimicry, but also provides a method to investigate the core processes involved in complex imitation. This is significant because, to date, research on complex imitation has been reliant on methods that assess the competence of infants, children, and nonhuman animals, but rarely afford carefully controlled, analytic investigation of the psychological processes underlying that competence.

This article has distinguished three ways in which aspects of the social and asocial context could, in principle, have an impact on automatic imitation via intentions: input modulation, where broadly attentional processes influence the extent of action stimulus processing; output modulation, where imitative motor representations are inhibited or allowed to gain control of overt behavior; and intervention, where context-dependent intentions have a direct effect on the process that converts activation of an action stimulus representation into activation of a topographically similar response representation. The review found evidence of input modulation and output modulation but not of intervention. This tripartite scheme could be of use in future studies of automatic imitation and also in research on the effects of contextual variables on motor mimicry and the mirror neuron system. For example, studies showing that out-group members are mimicked less than in-group members would ask whether this context effect is due to input modulation, output modulation, or intervention by social attitudes. However, success in future applications of this tripartite distinction will also require (a) theoretical models detailing exactly how a contextual variable might intervene between sensory and motor activation and (b) empirical studies designed explicitly to distinguish input and output modulation from intervention.

In addition to examining the automaticity and imitative character of automatic imitation, this review encompassed a substantial body of evidence that the long-term sensorimotor connections

mediating automatic imitation are established by associative learning. Insofar as automatic imitation is mediated by the mirror neuron system and continuous with motor mimicry, this evidence suggests that these phenomena may also be dependent on sensorimotor experience and subject to modification through learning-based interventions (Catmur et al., 2009; Chartrand & Van Baaren, 2009). Associative learning depends on temporal factors—the extent to which stimuli and responses occur together in time (contiguity) and are predictive of one another (contingency; Rescorla, 1968). Therefore, if automatic imitation depends on associative learning, it is defined by, but not at a deep level caused by, topographic similarity. It is defined by topographic similarity in that, by convention, a SRC effect counts as an automatic imitation effect only if it is attributable to the topographical relationship, rather than the spatial or symbolic relationship, between stimuli and responses. However, if not caused by topographic similarity in that the underlying learning process is blind to similarity; it will connect any pair of sensory and motor representations—topographically similar or dissimilar—that are contiguously and contingently activated. Priorities for future research in this area are to investigate whether the learning required for automatic imitation is constrained by genetic factors and to examine more closely the extent to which it depends on the same domain-general mechanisms that produce Pavlovian and instrumental conditioning.

Previous action research has shown that relatively uncontrolled processes can have a major impact on responses to inanimate stimuli (Kornblum et al., 1990), and studies of “the new unconscious” (Hassin et al., 2005), including motor mimicry, have suggested that this may also be true of social stimuli. However, the research reviewed in this article provides some of the strongest evidence to date that we are prone, in an unwilling and unreasoned way, to copy the actions of others.

References

- Aicken, M. D., Wilson, A. D., Williams, J. H., & Mon-Williams, M. (2007). Methodological issues in measures of imitative reaction times. *Brain and Cognition*, *63*, 304–308. doi:10.1016/j.bandc.2006.09.005
- Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, *26*, 2964–2970. doi:10.1523/JNEUROSCI.2921-05.2006
- Bach, P., Peatfield, N. A., & Tipper, S. P. (2007). Focusing on body sites: The role of spatial attention in action perception. *Experimental Brain Research*, *178*, 509–517. doi:10.1007/s00221-006-0756-4
- Bach, P., & Tipper, S. P. (2007). Implicit action encoding influences personal-trait judgments. *Cognition*, *102*, 151–178. doi:10.1016/j.cognition.2005.11.003
- Bailenson, J. N., & Yee, N. (2005). Digital chameleons: Automatic assimilation of nonverbal gestures in immersive virtual environments. *Psychological Science*, *16*, 814–819. doi:10.1111/j.1467-9280.2005.01619.x
- Barber, P., & O'Leary, M. (1997). The relevance of salience: Towards an activation account of irrelevant stimulus-response compatibility effects. In B. Hommel & W. Prinz (Eds.), *Theoretical issues in stimulus-response compatibility* (pp. 135–172). Amsterdam, the Netherlands: North-Holland. doi:10.1016/S0166-4115(97)80031-3
- Berger, S. M., & Hadley, S. W. (1975). Some effects of a model's performance on an observer's electromyographic activity. *American Journal of Psychology*, *88*, 263–276. doi:10.2307/1421596
- Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 210–225. doi:10.1037/0096-1523.32.2.210

- Bien, N., Roebroeck, A., Goebel, R., & Sack, A. T. (2009). The brain's intention to imitate: The neurobiology of intentional versus automatic imitation. *Cerebral Cortex*, *19*, 2338–2351. doi:10.1093/cercor/bhn251
- Bird, G., & Heyes, C. M. (2005). Effector-dependent learning by observation of a finger movement sequence. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 262–275. doi:10.1037/0096-1523.31.2.262
- Bird, G., Leighton, J., Press, C., & Heyes, C. M. (2007). Intact automatic imitation of human and robot actions in autism spectrum disorders. *Proceedings of the Royal Society of London*, *274*(B), 3027–3031. doi:10.1098/rspb.2007.1019
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22. doi:10.1016/S0001-6918(00)00024-X
- Brass, M., Bekkering, H., Wohlschlaeger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*, 124–143. doi:10.1006/brcg.2000.1225
- Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: A functional double dissociation. *Neuropsychologia*, *43*, 89–98. doi:10.1016/j.neuropsychologia.2004.06.018
- Brass, M., & Heyes, C. M. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*, 489–495. doi:10.1016/j.tics.2005.08.007
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 2359–2367. doi:10.1098/rstb.2009.0066
- Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage*, *14*, 1416–1423. doi:10.1006/nimg.2001.0944
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, *42*, 323–334. doi:10.1016/S0896-6273(04)00181-3
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, *21*, 667–684. doi:10.1017/S0140525X98001745
- Cannon, P. R., Hayes, A. E., & Tipper, S. P. (2009). An electromyographic investigation of the impact of task relevance on facial mimicry. *Cognition & Emotion*, *23*, 918–929. doi:10.1080/02699930802234864
- Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and performance XIX* (pp. 315–333). Oxford, England: Oxford University Press.
- Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008). Through the looking glass: Counter-mirror activation following incompatible sensorimotor learning. *European Journal of Neuroscience*, *28*, 1208–1215. doi:10.1111/j.1460-9568.2008.06419.x
- Catmur, C., & Heyes, C. M. (in press). Time course analyses confirm independence of automatic imitation and spatial compatibility effects. *Journal of Experimental Psychology: Human Perception and Performance*. doi:10.1037/a0019325
- Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. M. (in press). Making mirrors: Premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of Cognitive Neuroscience*. doi:10.1162/jocn.2010.21590
- Catmur, C., Walsh, V., & Heyes, C. M. (2007). Sensorimotor learning configures the human mirror system. *Current Biology*, *17*, 1527–1531. doi:10.1016/j.cub.2007.08.006
- Catmur, C., Walsh, V., & Heyes, C. M. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 2369–2380. doi:10.1098/rstb.2009.0048
- Chaminade, T., Franklin, D., Oztop, E., & Cheng, G. (2005). Motor interference between humans and humanoid robots: Effect of biological and artificial motion. In *Proceedings of the 4th IEEE International Conference on Development and Learning* (pp. 96–101). Osaka, Japan. doi:10.1109/DEVLRN.2005.1490951
- Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception–behavior link and social interaction. *Journal of Personality and Social Psychology*, *76*, 893–910. doi:10.1037/0022-3514.76.6.893
- Chartrand, T. L., & Van Baaren, R. (2009). Human mimicry. *Advances in Experimental Social Psychology*, *41*, 219–274. doi:10.1016/S0065-2601(08)00405-X
- Cho, Y. S., & Proctor, R. W. (2004). Influences of multiple spatial stimulus and response codes on orthogonal stimulus-response compatibility. *Perception & Psychophysics*, *66*, 1003–1017.
- Chong, T. T., Cunnington, R., Williams, M. A., & Mattingley, J. B. (2009). The role of selective attention in matching observed and executed actions. *Neuropsychologia*, *47*, 786–795. doi:10.1016/j.neuropsychologia.2008.12.008
- Chong, T. T., & Mattingley, J. B. (2009). Automatic and controlled processing within the mirror neuron system. In J. A. Pineda (Ed.), *Mirror neuron systems* (pp. 213–233). New York, NY: Humana Press. doi:10.1007/978-1-59745-479-7_10
- Cook, J., & Bird, G. (2010a). *Absent social modulation of the mirror neuron system in autism*. Manuscript submitted for publication.
- Cook, J., & Bird, G. (2010b). *Social attitudes differentially modulate imitation in adolescents and adults*. Manuscript submitted for publication.
- Cook, R., Press, C., Dickinson, A., & Heyes, C. M. (2010). Acquisition of automatic imitation is sensitive to sensorimotor contingency. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 840–852. doi:10.1037/a0019256
- Cosmides, L., & Tooby, J. (1994). Beyond intuition and instinct blindness: Toward an evolutionarily rigorous cognitive science. *Cognition*, *50*, 41–77. doi:10.1016/0010-0277(94)90020-5
- Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the response to hand pictures. *Neuropsychologia*, *40*, 492–502. doi:10.1016/S0028-3932(01)00134-8
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition*, *5*, 109–125. doi:10.1080/713756780
- Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *NeuroReport*, *8*, 347–349. doi:10.1097/00001756-199612200-00068
- Csibra, G. (2008). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance XX* (pp. 461–479). Oxford, England: Oxford University Press.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London, England: John Murray.
- De Jong, R., Liang, C.-C., & Lauber, E. (1994). Conditional and unconditional automaticity: A dual-process model of effects of spatial stimulus-response correspondence. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 731–750. doi:10.1037/0096-1523.20.4.731
- Dickinson, A., & Charnock, D. J. (1985). Contingency effects with maintained instrumental reinforcement. *Quarterly Journal of Experimental Psychology*, *37*(B), 397–416.
- Dimberg, U., Thunberg, M., & Elmehed, K. (2000). Unconscious facial reaction to emotional facial expressions. *Psychological Science*, *11*, 86–89. doi:10.1111/1467-9280.00221
- Dinstein, I., Hasson, U., Rubin, N., & Heeger, D. J. (2007). Brain areas selective for both observed and executed movements. *Journal of Neurophysiology*, *98*, 1415–1427. doi:10.1152/jn.00238.2007

- Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioral study in prehensile action. *Brain and Cognition*, *53*, 495–502. doi:10.1016/S0278-2626(03)00210-0
- Elbert, T., Pantev, C., Wienbruch, C., & Rockstroh, B. (1995, October 13). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307. doi:10.1126/science.270.5234.305
- Elsner, B., & Hommel, B. (2004). Contiguity and contingency in action effect learning. *Psychological Research*, *68*, 138–154. doi:10.1007/s00426-003-0151-8
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Ferrari, P. F., Bonini, L., & Fogassi, L. (2009). From monkey mirror neurons to primate behaviours: Possible “direct” and “indirect” pathways. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 2311–2323. doi:10.1098/rstb.2009.0062
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609. doi:10.1093/brain/119.2.593
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, *16*, 1824–1829. doi:10.1016/j.cub.2006.07.072
- Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*, 1674–1684. doi:10.1016/j.neuroimage.2007.02.003
- Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. M. (2008). Experience-based priming of body parts: A study of action imitation. *Brain Research*, *1217*, 157–170. doi:10.1016/j.brainres.2007.12.076
- Gowen, E., Stanley, J., & Miall, R. C. (2008). Movement interference in autism-spectrum disorder. *Neuropsychologia*, *46*, 1060–1068. doi:10.1016/j.neuropsychologia.2007.11.004
- Grèzes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “mirror” and “canonical” neurones in the human brain: An fMRI study. *NeuroImage*, *18*, 928–937. doi:10.1016/S1053-8119(03)00042-9
- Hassin, R. R., Uleman, J. S., & Bargh, J. A. (2005). *The new unconscious*. Oxford, England: Oxford University Press.
- Hedge, A., & Marsh, N. W. A. (1975). The effect of irrelevant spatial correspondence on two-choice response time. *Acta Psychologica*, *39*, 427–439. doi:10.1016/0001-6918(75)90041-4
- Hess, U., & Blairy, S. (2001). Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *International Journal of Psychology*, *40*, 129–141. doi:10.1016/S0167-8760(00)00161-6
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, *5*, 253–261. doi:10.1016/S1364-6613(00)01661-2
- Heyes, C. (2005). Imitation by association. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (pp. 157–176). Cambridge, MA: MIT Press.
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews*, *34*, 575–583. doi:10.1016/j.neubiorev.2009.11.007
- Heyes, C. M. (in press). What can imitation do for cooperation? In B. Calcott, R. Joyce, & K. Sterelny (Eds.), *Signalling, commitment, and cooperation*. Cambridge, MA: MIT Press.
- Heyes, C. M., & Bird, G. (2007). *Mirroring, association and the correspondence problem*. In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance XX* (pp. 461–479). Oxford, England: Oxford University Press.
- Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Brain Research Cognitive Brain Research*, *22*, 233–240. doi:10.1016/j.cogbrainres.2004.09.009
- Heyes, C. M., & Ray, E. (2000). What is the significance of imitation in animals? *Advances in the Study of Behavior*, *29*, 215–245. doi:10.1016/S0065-3454(08)60106-0
- Heyes, C., & Ray, E. D. (2004). Spatial S-R compatibility effects in an intentional imitation task. *Psychonomic Bulletin & Review*, *11*, 703–708.
- Hickok, G., & Hauser, M. (2010). (Mis)understanding mirror neurons. *Current Biology*, *20*, R593–R594. doi:10.1016/j.cub.2010.05.047
- Hommel, B. (1996). S–R compatibility effects without response uncertainty. *Quarterly Journal of Experimental Psychology*, *49(A)*, 546–571. doi:10.1080/027249896392496
- Hommel, B. (2000). The prepared reflex: Automaticity and control in stimulus-response translation. In S. Monsell & J. Driver (Eds.), *Control of cognitive processes: Attention and performance XVIII* (pp. 247–273). Oxford, England: Oxford University Press.
- Hove, M. J., & Risen, J. L. (2009). It’s all in the timing: Interpersonal synchrony increases affiliation. *Social Cognition*, *27*, 949–960. doi:10.1521/soco.2009.27.6.949
- Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*, 653–670. doi:10.1146/annurev.psych.60.110707.163604
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999, December 24). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.
- Jansson, E., Wilson, A. D., Williams, J. H., & Mon-Williams, M. (2007). Methodological problems undermine tests of the ideomotor conjecture. *Experimental Brain Research*, *182*, 549–558. doi:10.1007/s00221-007-1013-1
- Kilner, J., Hamilton, A. F., & Blakemore, S. J. (2007). Interference effect of observed human movement on action is due to velocity profile of biological motion. *Social Neuroscience*, *2*, 158–166. doi:10.1080/17470910701428190
- Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2010). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience*, *29*, 10153–10159. doi:10.1523/JNEUROSCI.2668-09.2009
- Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology*, *13*, 522–525. doi:10.1016/S0960-9822(03)00165-9
- Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus-response compatibility—A model and taxonomy. *Psychological Review*, *97*, 253–270. doi:10.1037/0033-295X.97.2.253
- Lakin, J. L., & Chartrand, T. L. (2003). Using unconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, *14*, 334–339. doi:10.1111/1467-9280.14481
- Leighton, J., Bird, G., Orsini, C., & Heyes, C. M. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology*, *46*, 905–910. doi:10.1016/j.jesp.2010.07.001
- Leighton, J., & Heyes, C. M. (2010). Hand to mouth: Automatic imitation across effector systems. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 1174–1183. doi:10.1037/a0019953
- Liepelt, R., & Brass, M. (2010). Top-down modulation of motor priming by belief about animacy. *Experimental Psychology*, *57*, 221–227. doi:10.1027/1618-3169/a000028
- Liepelt, R., von Cramon, D. Y., & Brass, M. (2008). What is matched in direct matching? Intentional attribution modulates motor priming. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 578–591. doi:10.1037/0096-1523.34.3.578
- Likowski, K. U., Muhlberger, A., Seibt, B., Pauli, P., & Weyers, P. (2008). Modulation of facial mimicry by attitudes. *Journal of Experimental Social Psychology*, *44*, 1065–1072. doi:10.1016/j.jesp.2007.10.007
- Longo, M. R., & Bertenthal, B. I. (2009). Attention modulates the specificity of automatic imitation to human actors. *Experimental Brain Research*, *192*, 739–744. doi:10.1007/s00221-008-1649-5

- Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically possible and impossible actions: Effects of priming movements versus goals. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 489–501. doi:10.1037/0096-1523.34.2.489
- Massen, C., & Prinz, W. (2009). Movements, actions and tool-use actions: An ideomotor approach to imitation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 2349–2358. doi:10.1098/rstb.2009.0059
- Meltzoff, A. N., & Moore, M. K. (1997). Explaining facial imitation: A theoretical model. *Early Development and Parenting*, *6*, 179–192. doi:10.1002/(SICI)1099-0917(199709/12)6:3/4<179::AID-EDP157>3.0.CO;2-R
- Merzenich, M. M., Nelson, R. J., Stryker, M. P., Cynader, M. S., Schopma, A., & Zook, J. M. (1984). Somatosensory cortical map changes following digit amputation in adult monkeys. *Journal of Comparative Neurology*, *224*, 591–605. doi:10.1002/cne.902240408
- Neumann, O. (1984). Automatic processing: A review of recent findings and a plea for an old theory. In W. Prinz & A. F. Sanders (Eds.), *Cognition and motor processes* (pp. 255–293). Berlin, Germany: Springer-Verlag.
- Ocampo, B., & Kritikos, A. (2010). Placing actions in context: Motor facilitation following observation of identical and non-identical manual acts. *Experimental Brain Research*, *201*, 743–751. doi:10.1007/s00221-009-2089-6
- Pawlby, S. J. (1977). Imitative interaction. In H. Schaffer (Ed.), *Studies in mother-infant interaction* (pp. 203–224). New York, NY: Academic Press.
- Pearce, J. M. (1987). A model of stimulus generalization in Pavlovian conditioning. *Psychological Review*, *94*, 61–73. doi:10.1037/0033-295X.94.1.61
- Pinker, S. (1997). *How the mind works*. London, England: Penguin Press.
- Posner, M. I. (1978). *Chronometric explorations of the mind*. Hillsdale, NJ: Erlbaum.
- Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Brain Research Cognitive Brain Research*, *25*, 632–640. doi:10.1016/j.cogbrainres.2005.08.020
- Press, C., Bird, G., Walsh, E., & Heyes, C. (2008). Automatic imitation of intransitive actions. *Brain and Cognition*, *67*, 44–50. doi:10.1016/j.bandc.2007.11.001
- Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of imitation by human and robotic models. *European Journal of Neuroscience*, *24*, 2415–2419. doi:10.1111/j.1460-9568.2006.05115.x
- Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2509–2514. doi:10.1098/rspb.2007.0774
- Press, C., Heyes, C. M., & Kilner, J. M. (in press). Learning to understand others' actions. *Biology Letters*. doi:10.1098/rsbl.2010.0850
- Prinz, W. (2005). An ideomotor approach to imitation. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (pp. 141–156). Cambridge, MA: MIT Press.
- Proctor, R. W., & Vu, K.-P. L. (2006). *Stimulus-response compatibility principles: Data, theory and application*. Boca Raton, FL: Taylor & Francis.
- Ray, E. D., & Heyes, C. M. (2011). Imitation in infancy: The wealth of the stimulus. *Developmental Science*, *14*, 92–105. doi:10.1111/j.1467-7687.2010.00961.x
- Rescorla, R. A. (1968). Probability of shock in the presence and absence of CS in fear conditioning. *Journal of Comparative and Physiological Psychology*, *66*, 1–5. doi:10.1037/h0025984
- Sellars, W., Rorty, R., & Brandom, R. (1997). *Empiricism and the philosophy of mind*. Cambridge, MA: Harvard University Press.
- Shanks, D. R., & Dickinson, A. (1991). Instrumental judgment and performance under variations in action-outcome contingency and contiguity. *Memory & Cognition*, *19*, 353–360.
- Shiffrin, R., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review*, *84*, 127–190. doi:10.1037/0033-295X.84.2.127
- Shmuelof, L., & Zohary, E. (2006). A mirror representation of others' actions in the human anterior parietal cortex. *Journal of Neuroscience*, *26*, 9736–9742. doi:10.1523/JNEUROSCI.1836-06.2006
- Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology*, *81*, 174–176. doi:10.1037/h0027448
- Spengler, S., Brass, M., Kuhn, S., & Schutz-Bosbach, S. (2010). Minimizing motor mimicry by myself: Self-focus enhances online action-control mechanisms during motor contagion. *Consciousness and Cognition*, *19*, 98–106. doi:10.1016/j.concog.2009.12.014
- Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: Control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *Social Neuroscience*, *5*, 401–416.
- Squareman, C. (1916). *My book of indoor games*. Chicago, IL: The Chicago Park Commission.
- Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference during observation of a moving dot stimulus. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 915–926. doi:10.1037/0096-1523.33.4.915
- Stel, M., Blascovich, J., McCall, C., Mastop, J., Van Baaren, R. B., & Vonk, R. (2010). Mimicking disliked others: Effects of a priori liking on the mimicry-liking link. *European Journal of Social Psychology*, *40*, 867–880. doi:10.1002/ejsp.655
- Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: A transcranial magnetic stimulation study. *NeuroReport*, *11*, 2289–2292. doi:10.1097/00001756-200007140-00044
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662. doi:10.1037/h0054651
- Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1746–1759. doi:10.1037/0096-1523.26.6.1746
- Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture* (pp. 319–346). New York, NY: Academic Press. doi:10.1016/B978-012273965-1/50016-9
- Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 830–846. doi:10.1037/0096-1523.24.3.830
- van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science*, *15*, 71–74. doi:10.1111/j.0963-7214.2004.01501012.x
- van Baaren, R. B., Maddux, W. W., Chartrand, T. L., De Bouter, C., & van Knippenberg, A. (2003). It takes two to mimic: Behavioral consequences of self-construals. *Journal of Personality and Social Psychology*, *84*, 1093–1102. doi:10.1037/0022-3514.84.5.1093
- van Schie, H. T., van Waterschoot, B. M., & Bekkering, H. (2008). Understanding action beyond imitation: Reversed compatibility effects of action observation in imitation and joint action. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 1493–1500. doi:10.1037/a0011750
- Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: Perspective matters. *Neuropsychologia*, *41*, 941–951. doi:10.1016/S0028-3932(02)00319-6
- Wang, Y., Newport, R., & Hamilton, A. (in press). Eye contact enhances mimicry of intransitive hand movements. *Biology Letters*. doi:10.1098/rsbl.2010.0279
- Washburn, M. F. (1908). *The animal mind*. New York, NY: Macmillan.

Weeks, D. J., & Proctor, R. W. (1990). Salient features coding in the translation between orthogonal stimulus and response dimensions. *Journal of Experimental Psychology: General*, *119*, 355–366. doi:10.1037/0096-3445.119.4.355

Wiggett, A. J., Hudson, M., Tipper, S. P., & Downing, P. E. (in press). Learning associations between action and perception: Effects of incompatible training on body part and spatial priming. *Brain & Cognition*.

Williams, J. H., Waite, G. D., Gilchrist, A., Perrett, D. I., Murray, A. D., & Whiten, A. (2006). Neural mechanisms of imitation and “mirror

neuron” functioning in autistic spectrum disorder. *Neuropsychologia*, *44*, 610–621. doi:10.1016/j.neuropsychologia.2005.06.010

Zorzi, M., & Umiltà, C. (1995). A computational model of the Simon effect. *Psychological Research*, *58*, 193–205. doi:10.1007/BF00419634

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