

Evolution, development and intentional control of imitation

Cecilia Heyes

Phil. Trans. R. Soc. B 2009 **364**, 2293-2298

doi: 10.1098/rstb.2009.0049

References

[This article cites 25 articles, 3 of which can be accessed free](#)

<http://rstb.royalsocietypublishing.org/content/364/1528/2293.full.html#ref-list-1>

Rapid response

[Respond to this article](#)

<http://rstb.royalsocietypublishing.org/letters/submit/royptb;364/1528/2293>

Subject collections

Articles on similar topics can be found in the following collections

[neuroscience](#) (256 articles)

[behaviour](#) (925 articles)

[cognition](#) (239 articles)

[developmental biology](#) (116 articles)

[evolution](#) (1225 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Introduction

Evolution, development and intentional control of imitation

Cecilia Heyes*

*All Souls College and Department of Experimental Psychology, University of Oxford,
Oxford OX1 4AL, UK*

Imitation is at the heart of social cognitive neuroscience. It is a neurocognitive process that bridges the gap between minds; powers cognitive and social development; promotes cooperation and well-being; and provides a channel of cultural inheritance. The papers in this theme issue review cutting-edge research on imitation and report original data using all of the principal methodologies, including comparative, developmental, cognitive-behavioural and neurological techniques. This paper introduces these interdisciplinary contributions and, proposing that the field currently has four inter-related foci—correspondence, control, cooperation and cultural inheritance—offers an overview of the state-of-the-art in research on the mechanisms and functions of imitation.

Keywords: imitation; mirror system; correspondence problem; cognitive control; cooperation; cultural inheritance

Social cognitive neuroscience is an exciting, interdisciplinary venture that explains in an integrated way the neural, evolutionary and experiential processes that allow us to understand and to communicate with one another (Blakemore *et al.* 2004). Imitation is at the heart of this new venture. It seems to be simple—we copy the body movements of others easily, without deliberation, all the time—but imitation is an important and intriguing neurocognitive process: a process that bridges the gap between one mind and another; that powers cognitive and social development in infancy and childhood; that promotes empathy, cooperation and well-being in our relationships with others; and provides a channel of evolutionary, cultural inheritance that makes us distinctively human.

Imitation is a key focus of research in social cognitive neuroscience, not only because it plays a crucial role in social cognition, but also because it is a field in which the groundwork for successful interdisciplinary research has already been laid. The many facets of imitation have been studied for more than a century by social, developmental and comparative psychologists, evolutionary biologists and neurologists. These groups typically worked in mutual isolation, but when the social cognitive neuroscience initiative began some 10 years ago, they were poised to take a leading role. Their studies of imitation in animals, children and patients with brain damage provided a store of valuable information, and they were fired by two important discoveries: *mirror neurons*, cells in the monkey brain that respond both when an action is executed and when the same action is observed (Gallese *et al.* 1996), and *automatic imitation*

(or *mimicry*), imitative behaviour in healthy adults that is not intended (Stürmer *et al.* 2000) and of which the imitator may be unaware (Chartrand & Bargh 1999). In addition, new methodologies—brain imaging, transcranial magnetic stimulation and innovative reaction time procedures—have made it possible for the first time to study the neurological and psychological mechanisms of imitation as they operate in the most adept imitators—healthy adult humans.

The powerful effects of these innovations were just beginning to be felt in 2002 when a major conference, ‘Perspectives on Imitation’, was held in Royaumont, France (the proceedings were published in Hurley & Chater 2005). This Theme Issue provides an overview of the most important advances in imitation research since that meeting, integrating insights gained through the use of the old and the new methodologies, and summarizing the state of play with respect to key questions about the mechanisms and functions of imitation. This article introduces each of the papers in the Theme Issue through discussion of four cross-cutting foci of enquiry, and in an overview of the Issue’s structure.

1. FOCI

Two of the cross-cutting issues, correspondence and control, relate primarily to the cognitive and neural mechanisms that make imitation possible; the other two, cooperation and cultural inheritance, concern the functions of imitation.

(a) *Correspondence*

At the core of imitation research is a unique and surprisingly intractable problem: how does the mind/brain convert an observed into an enacted body movement? The depth of this *correspondence problem* is most apparent in the imitation of perceptually opaque actions, such as

*cecilia.heyes@all-souls.ox.ac.uk

One contribution of 13 to a Theme Issue ‘Evolution, development and intentional control of imitation’.

facial expressions and whole-body movements; actions that look and feel very different when they are observed and executed (Heyes & Ray 2000). For example, if you watch me raising my eyebrows, you see two arcs (the brows) moving upwards on an ellipse (the face), but you do not receive any distinctive sensations from the muscles of your face. In contrast, if you raise your eyebrows, you feel them moving, but you do not receive any distinctive visual input. Under circumstances such as these—where, from a first person perspective, the observed and executed actions are very different—how does your neurocognitive system translate the observed movement into a corresponding action; into behaviour that looks, from a third party perspective, the same as mine?

In the past it was widely assumed that the correspondence problem was solved by effortful, symbolic (or rule-governed) processes. These processes were thought to operate only when the observer intended to imitate and, although their rules were not specified, it was assumed that they could bridge the gap between otherwise distinct perceptual and motor representations of action (e.g. Bandura 1977; Meltzoff & Moore 1997). In one of the most dramatic scientific developments in recent years, this *symbolic* view has been largely superseded by an *embodied* view of imitation. Research on the mirror system (Bastiaansen *et al.* 2009; Ferrari *et al.* 2009) and automatic imitation (Catmur *et al.* 2009; van Baaren *et al.* 2009), much of it inspired by ideomotor theory (Massen & Prinz 2009), has shown that action perception and action production are enduringly and intimately related. Even when we do not intend to imitate, the perception of action activates the same neural (mirror neurons or *mirror areas*) and representational (*common codes, shared representations* or *vertical associations*) structures that are involved in the production of the perceived action. This suggests that, rather than being distantly related by rules, the perception and the execution of action depend on the same systems, and the potential or impulse to produce an imitative action is generated, not just when I want to imitate, but whenever I watch another person's behaviour.

The discovery of mirror neurons and common codes—bimodal structures that are active during observation and execution of the same action—is understood by many researchers to provide a potential solution to the correspondence problem (e.g. Ferrari *et al.* 2009; Huber *et al.* 2009; Massen & Prinz 2009; Rumiati *et al.* 2009). Others regard these discoveries as a force that moves the correspondence problem to a new level, challenging us to explain how mirror neurons and common codes, rather than whole brains or minds, convert an observed into an enacted body movement. The associative sequence learning (ASL) theory of imitation suggests that the solution to both the original and the newer versions of the correspondence problem is sensorimotor learning (Heyes 2001). Studies of infant development, training and expertise suggest that, rather than being innate, structures such as mirror neurons and common codes develop through correlated experience of observing and executing actions (Catmur *et al.* 2009).

(b) *Control*

The symbolic view implied that, in each episode of imitation, a controlled cognitive process solves the

correspondence problem from scratch, by mapping a perceptual representation of the observed action onto a normally separate and distinct motor representation of the same action. Now we know that many perceptual and motor features of action are represented together, in bimodal structures, the question of how imitation is controlled has a new focus. When these bimodal structures are present, the perception of action leads automatically to the activation of corresponding motor codes and thereby to the impulse or potential to imitate (Massen & Prinz 2009). Therefore, control is needed, not to solve the correspondence problem and to launch an imitative act, but to ensure that imitative behaviour is goal directed rather than compulsive (Brass *et al.* 2009; Rumiati *et al.* 2009).

Leading contemporary research on the control of imitation, Brass and his associates have shown that two cortical structures, which are also involved in attributing mental states to others, play a crucial role (Brass *et al.* 2009). Their work indicates that the temporo-parietal junction is important in distinguishing the agent's own acts from those of others, and that the anterior fronto-medial cortex allows the agent's own intention to be enforced when it is in conflict with an elicited, imitative response. These control functions are particularly interesting because they appear to be specialized for social interaction. However, at least in healthy adult humans, general executive processes—of the kind that mediate inhibition, working memory and sequence processing in a range of non-social tasks—are also involved in the regulation of imitative performance (Ferrari *et al.* 2009; Rumiati *et al.* 2009). Indeed, Rumiati and colleagues suggest that, except in specified cases of neurological damage, adult human imitation is always *strategic* in at least one sense: executive processes determine whether observed actions are processed via large-scale, semantic representations of action, or as a series of relatively meaningless action fragments.¹

Control is also an important issue in the literature on imitation in children and non-human animals. Some investigators regard control as such an important feature of imitation that they prefer to use a different term, such as *mimicry* (Tomasello 1996) or *response facilitation* (Byrne 2003) to refer to body movement copying that is relatively uncontrolled (Ferrari *et al.* 2009; Tennie *et al.* 2009). For many decades, those studying imitation in children and animals focused on controlled, *intentional* or *true* imitation because it was thought that imitation must be controlled in order to play an important role in cognitive and social development, and to mediate cultural inheritance. This assumption is now under review (Huber *et al.* 2009) as research on the Chameleon effect in adults (Chartrand & Bargh 1999; van Baaren *et al.* 2009) and 'over-copying' in children (Whiten *et al.* 2009) suggests that, even when control is limited, imitation can have systematic and far-reaching effects on cooperative behaviour and the potential for cultural evolution.²

(c) *Cooperation*

Anecdotal reports and folk wisdom have long suggested that, when they are in conversation, adults inadvertently copy each other's gestures and mannerisms, and that

this tendency somehow smoothes their interaction. In the last 10 years, research on this kind of imitation—known as the *Chameleon effect* (Chartrand & Bargh 1999), *non-conscious mimicry* (van Baaren *et al.* 2009) or automatic imitation (Leighton *et al.* in press)—has made enormous progress. Carefully controlled experiments in semi-naturalistic settings have confirmed that the effect is pervasive, and that post-interaction interviews provide no evidence that imitatees are aware of being copied, or that imitators are aware of, or intend to, imitate. Yet more important, these experiments have shown that, although pervasive and unintentional, this kind of imitation is systematically related to prosocial attitudes and behaviour (van Baaren *et al.* 2009). Broadly speaking, there is a virtuous circle in which a cooperative frame of mind makes me more likely to imitate you, and being imitated by me enhances your prosocial attitudes, making you more likely to help me and others.

Cutting-edge research on the way in which the brain *mirrors*, not only the actions of others, but also their emotions and sensations, further underlines the importance of imitation with respect to cooperation by showing that similar mechanisms mediate imitation and empathy (Bastiaansen *et al.* 2009). The current focus in this new field is on identifying the states—disgust, pain, fear—that evoke similar neural responses when they are experienced by the subject, and when they are detected in another person. Future research in this growth area will, no doubt, examine the connections among imitation- and empathy-related networks, and relate these both to the cooperative functions of imitation, and to the impact of cooperation on cultural inheritance (Tennie *et al.* 2009).

(d) *Cultural inheritance*

It has been clear for more than a century that imitation of some kind provides a non-genetic route for the inheritance of phenotypic attributes, and has the potential to support the *cumulative* properties of human culture—the conservation and dissemination of innovations in ways that allow technologies and practices to improve over time. The issues that are unclear concern: (i) the type of imitation that has this potential and (ii) its importance, relative to other cognitive and social attributes, in supporting cumulative culture. These questions are particularly active foci of debate in research comparing the imitative behaviour of children and chimpanzees (Tennie *et al.* 2009; Whiten *et al.* 2009).

Regarding types of imitation, it is generally agreed that, to support cumulative culture, imitation must achieve a significant degree of copying fidelity, and involve or enable learning, i.e. the acquisition of novel behaviour. Traditionally, it has been assumed that imitation involving the performance of a novel behaviour, *imitation learning*, is fundamentally different from mimicry, the copying of body movements that were part of the imitator's motor repertoire before they were imitated (e.g. Thorndike 1898). Imitation learning and mimicry were thought to depend on distinct neurocognitive processes that solve the correspondence problem in different ways, and to

have largely independent evolutionary histories and developmental trajectories. This view still has many authoritative adherents, including many experts on imitation in non-human primates. However, now there is also a growing body of theory and evidence suggesting that mimicry and imitation learning are continuous; that the same bimodal structures solve the correspondence problem in both cases, while imitation learning enlists additional, general purpose mechanisms of learning and cognitive control—mechanisms that evolved for sensory and motor sequence processing, rather than for imitation specifically (Heyes & Ray 2000; Catmur *et al.* 2009; Huber *et al.* 2009; Massen & Prinz 2009; Rumiati *et al.* 2009; Shea 2009). If the traditional view is correct, only one, extraordinary type of imitation can contribute to cumulative cultural inheritance, and it is distinct from the type of imitation—the automatic kind—examined in many of the papers in this Theme Issue. If the emerging view is correct, imitation is a more unitary phenomenon, and, as Shea's paper illustrates, all contemporary research in the field has a potential bearing on the question of whether imitation is an important mechanism of cultural inheritance.

The importance of imitation relative to other social and cognitive attributes is a matter of some controversy. Tomasello and his associates in Leipzig argue that, in enabling cumulative culture, imitation or *process-oriented copying* (copying of body movements) is much more important than *emulation* or *product-oriented copying* (copying the effects of body movements on environmental objects), because imitation supports a higher level of copying fidelity (Tennie *et al.* 2009). In contrast, Whiten and colleagues in St Andrews point out that both imitation and emulation can involve high fidelity copying, and therefore deny that imitation is unique among processes of social learning in its capacity to support cultural inheritance (Whiten *et al.* 2009). This debate is closely related to the question of whether cumulative cultural change occurs in free-living chimpanzee populations. If emulation can also support high-fidelity copying, then experimental demonstrations, not only of imitation, but also of emulation in chimpanzees, make it more plausible that geographical variations in the behaviour of free-living apes are due to cumulative cultural change (Whiten *et al.* 1999).

Although the two groups, in Leipzig and St Andrews, that lead research on cultural learning are divided on many issues, they are both beginning to stress the role of group wisdom rather than individual rationality in generating cumulative cultural change. In the 1990s, it was thought that, in order to mediate high-fidelity cultural inheritance, imitation must be combined with considerable insight into the minds of others and the operation of physical systems. It was assumed that, to support cumulative culture, imitators must select for reproduction of those features of observed body movement that were intended by the model (rather than accidental), and that make sense in the physical and social context in which the action is observed. However, recent evidence of 'over-imitation' or 'over-copying' in children, relative to chimpanzees (Whiten *et al.* 2009)—the reproduction of incidental and apparently irrelevant features of

observed action—has led to a new emphasis on the importance of social processes, rather than individual rationality. Tennie *et al.* (2009) emphasize the roles of active teaching and social norms in ensuring faithful copying, while Whiten *et al.* (2009) raise the possibility that children over-imitate because this behaviour has been a focus of social rewards during development.

In summary: drawing on the full range of resources in social cognitive neuroscience, the papers in this Theme Issue provide new perspectives on each of the four principal foci of research on imitation—correspondence, control, cooperation and cultural inheritance. These issues are not only cross-cutting—each is being tackled using an interdisciplinary range of methods—but also inter-related. For example, research indicating that embodied, sensorimotor mechanisms solve the correspondence problem has re-oriented studies of control. These studies are now showing us how imitative acts are blocked, rather than seeking processes of initiation. Similarly, a deeper understanding of correspondence and control, combined with insights from the study of imitation in chimpanzees, and in humans in naturalistic social settings, is enabling the integration of research on the mechanisms and functions of imitation. We are beginning to understand how cultural learning contributes to solving the correspondence problem, and that weakly controlled as well as highly controlled imitation can both promote cooperation and support cultural inheritance.

2. STRUCTURE

Although research on imitation is becoming increasingly integrated, for convenience this Theme Issue is divided into two principal parts. The papers in the first section are concerned primarily with the cognitive and neurological mechanisms that make it possible for observed body movements to be converted into enacted body movements (correspondence problem), and that channel the output from these mechanisms so that imitation can be purposeful or goal directed rather than merely compulsive (control). The papers in the second section are primarily concerned with the functions of imitation in day-to-day social interaction (cooperation), and the role of imitation in supporting evolutionary, cultural change (cultural inheritance). Most of the papers contain both an incisive review of the recent literature in their field and important, original data.

Each of the first six articles, on mechanisms of imitation, surveys and contributes to research using a distinctive methodology. Huber *et al.* (2009) focus on behavioural studies of non-human animals, highlighting recent evidence of selective imitation in dogs, and high-fidelity imitation in monkeys (Voelkl & Huber 2007)—species that were not previously thought to be capable of imitation. The paper by Ferrari *et al.* (2009) takes a fresh look at the implications of the single-unit recording studies that revealed mirror neurons in monkeys, and, guided by recent evidence of facial gesture imitation in newborn monkeys, distinguishes two ways in which these bimodal structures could contribute to imitative behaviour. Jones (2009) takes up the theme of neonatal imitation

and offers both a detailed critique of research on imitation in human newborns, and a survey of recent evidence on the development of imitation in later infancy. Both components emphasize the importance of dynamic processes of sensorimotor learning in the early development of imitation.

With the papers by Rumiati *et al.* (2009), Massen & Prinz (2009) and Brass *et al.* (2009), the spotlight moves from comparative and developmental research to studies of imitation in adult humans. Drawing on a long tradition of research in neuropsychology, Rumiati and colleagues examine the current status of the dual-route model of imitation, and what studies of people with brain damage tell us about the role of *body schemas* in solving the correspondence problem. Massen & Prinz (2009) review the abundance of recent behavioural studies that have used innovative reaction time procedures. These *compatibility procedures*, originally developed by Prinz's group in Munich and Leipzig, and now used across the world, are revealing the functional properties of the bimodal structures that mediate imitation. *Ideomotor theory* captures many of these properties but, motivated by original data presented in their paper, Massen & Prinz argue that the theory needs expansion to take account of mechanisms that modulate or control the basic bimodal structures. Picking up on this theme, and using some of the same compatibility paradigms in combination with brain imaging, Brass *et al.* show that imitation is controlled by specialized processes of discrimination and inhibition involving the temporo-parietal junction and the anterior fronto-median cortex.

The final paper in the first section, by Catmur *et al.* (2009), is synthetic; expanding the evidence base of the ASL model, their paper draws on research using all of the principal methodologies—comparative, developmental, cognitive and brain imaging—to make the case that, rather than having 'evolved', the bimodal structures that solve the correspondence problem are products of associative, sensorimotor learning. This paper also links the first section of the Theme Issue, on neurocognitive mechanisms of imitation, with the second section, on social and cultural functions of imitation, by suggesting that associative learning mechanisms use sociocultural input to build mirror neurons and other shared representations.

The second section of the Theme Issue includes two pairs of papers and a final, integrative analysis. In the first pair, by van Baaren *et al.* (2009) and Bastiaansen *et al.* (2009), our attention is focused on the way in which imitation draws people together and, tessellated with empathetic emotional processes, lays the foundations for the extraordinary degree of cooperation that characterizes human social life (Sterelny 2003). Van Baaren *et al.* (2009) review the variables that modulate mimicry in naturalistic social settings and show that, with telling exceptions, mimicry of this kind promotes positive social attitudes, not only in relation to the imitator, but also towards other agents. Bastiaansen *et al.* (2009) survey pioneering work, much of it from the senior author's laboratory, on the neural mechanisms that enable us to share the sensations and emotional states of others. They examine the interplay between imitation

or *motor simulation* and empathy or *emotional mirroring*, and linking their paper with the issue of control, raise the question of how each of these processes interact with semantic knowledge.

The authors of the second pair of papers come from the two groups that lead research on imitation and cultural inheritance in chimpanzees. Their papers represent an ongoing exchange, driven by argument and evidence, about the possibility of culture in non-human animals, and the role that imitation plays in making human lives unique. Tennie *et al.* (2009) unveil an important new idea in this debate, the *zone of latent solutions*, while Whiten *et al.* (2009) present evidence that chimpanzees have the kind of social learning resources implicated in cultural inheritance.

The final paper offers a new framework for research on imitation (Shea 2009). It first examines the features that imitation would need in order, not only to function as an inheritance system, but to have evolved as an inheritance system; to have been favoured by natural selection because it promotes the inheritance of behaviour. Shea then draws on a remarkably wide range of recent research—bearing on both the mechanisms and functions of imitation—to ask whether imitation has these features. Naturally, this is provisional analysis; additional work would be needed to provide a definitive answer to this question, and one of the strengths of Shea's integrative approach is that it suggests new empirical questions. However, as with many of the questions about imitation that have challenged psychologists and biologists for more than a century, current work in social cognitive neuroscience both reflects and generates well-founded confidence that they are now, at last, in the process of resolution.

This volume arose from a meeting on 'The evolution, development and intentional control of imitation', held in March 2008, hosted by the University of Vienna and funded by the European Community's Sixth Framework Programme under contract number NEST 012929. The co-editors would like to express their thanks to all those who contributed to that meeting. Preparation of this article was supported by the Economic and Social Research Council's (ESRC) research centre for Economic Learning and Social Evolution (ELSE). I am grateful to my co-editors and to Geoff Bird, Caroline Catmur and Clare Press for their comments.

ENDNOTES

¹There are several 'two-route' proposals in the current literature on imitation. Tessari & Rumiati's (2004) 'dual-route' model of imitation is consonant with Heyes' (2001) proposal that bimodal structures can be formed via linguistic and non-linguistic routes (although, confusingly, Heyes labels the linguistic route 'indirect' while Tessari & Rumiati call it 'direct'). The direct and indirect routes delineated by Ferrari *et al.* (2009) do not relate in any simple way to those distinguished by Tessari & Rumiati's dual-route model.

²Those who study children, domestic animals and non-human primates typically describe imitation and related behaviour as if it were strategic or controlled (Huber *et al.* 2009; Tennie *et al.* 2009; Whiten *et al.* 2009). For example, subjects are consistently portrayed as 'selecting' or 'choosing' courses of action, when their behaviour might instead be elicited by the stimulus context. In most cases this is purely conventional; it is not based on experimental evidence that the behaviour is controlled rather than automatic, and does not constitute a claim to that effect. Studies of control and automaticity in the imitation of laboratory species have had mixed results (Mui *et al.* 2008).

REFERENCES

- Bandura, A. 1977 *Social learning theory*. Englewood Cliffs, NJ: Prentice Hall.
- Bastiaansen, J. A. C. J., Thioux, M. & Keysers, C. 2009 Evidence for mirror systems in emotions. *Phil. Trans. R. Soc. B* **364**, 2391–2404. (doi:10.1098/rstb.2009.0058)
- Blakemore, S. -J., Winston, J. & Frith, U. 2004 Social cognitive neuroscience: where are we heading? *Trends Cogn. Sci.* **8**, 216–222. (doi:10.1016/j.tics.2004.03.012)
- Brass, M., Ruby, P. & Spengler, S. 2009 Inhibition of imitative behaviour and social cognition. *Phil. Trans. R. Soc. B* **364**, 2359–2367. (doi:10.1098/rstb.2009.0066)
- Byrne, R. W. 2003 Imitation as behaviour parsing. *Phil. Trans. R. Soc. Lond. B* **358**, 529–536. (doi:10.1098/rstb.2002.1219)
- Catmur, C., Walsh, V. & Heyes, C. 2009 Associative sequence learning: the role of experience in the development of imitation and the mirror system. *Phil. Trans. R. Soc. B* **364**, 2369–2380. (doi:10.1098/rstb.2009.0048)
- Chartrand, T. L. & Bargh, J. A. 1999 The chameleon effect: the perception–behavior link and social interaction. *J. Pers. Soc. Psychol.* **76**, 93–910. (doi:10.1037/0022-3514.76.6.893)
- Ferrari, P. F., Bonini, L. & Fogassi, L. 2009 From monkey mirror neurons to primate behaviours: possible 'direct' and 'indirect' pathways. *Phil. Trans. R. Soc. B* **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)
- Heyes, C. 2001 Causes and consequences of imitation. *Trends Cogn. Sci.* **5**, 253–261. (doi:10.1016/S1364-6613(00)01661-2)
- Heyes, C. M. & Ray, E. D. 2000 What is the significance of imitation in animals? *Adv. Study Behav.* **29**, 215–245. (doi:10.1016/S0065-3454(08)60106-0)
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z. & Miklósi, A. 2009 The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? *Phil. Trans. R. Soc. B* **364**, 2299–2309. (doi:10.1098/rstb.2009.0060)
- Hurley, S. & Chater, N. 2005 *Perspectives on imitation: from neuroscience to social science*. Cambridge, MA: MIT Press.
- Jones, S. S. 2009 The development of imitation in infancy. *Phil. Trans. R. Soc. B* **364**, 2325–2335. (doi:10.1098/rstb.2009.0045)
- Leighton, J., Bird, G., Orsini, C. & Heyes, C. M. In press. Social attitudes modulate automatic imitation. *J. Exp. Soc. Psychol.*
- Massen, C. & Prinz, W. 2009 Movements, actions, and tool-use actions: an ideomotor approach to imitation. *Phil. Trans. R. Soc. B* **364**, 2349–2358. (doi:10.1098/rstb.2009.0059)
- Meltzoff, A. N. & Moore, M. K. 1997 Explaining facial imitation: a theoretical model. *Early Dev. Parent.* **6**, 179–192. (doi:10.1002/(SICI)1099-0917(199709/12)6:3/4<179::AID-EDP157>3.0.CO;2-R)
- Mui, R., Haselgrove, M., Pearce, J. M. & Heyes, C. M. 2008 Automatic imitation in budgerigars. *Proc. R. Soc. B* **275**, 2547–2553. (doi:10.1098/rspb.2008.0566)
- Rumiati, R. I., Carmo, J. C. & Corradi-Dell'Acqua, C. 2009 Neuropsychological perspectives on the mechanisms of imitation. *Phil. Trans. R. Soc. B* **364**, 2337–2347. (doi:10.1098/rstb.2009.0063)
- Shea, N. 2009 Imitation as an inheritance system. *Phil. Trans. R. Soc. B* **364**, 2429–2443. (doi:10.1098/rstb.2009.0061)
- Sterelny, K. 2003 *Thought in a hostile world: the evolution of human cognition*. Chichester, UK: Blackwell Publishing.

- Stürmer, B., Aschersleben, G. & Prinz, W. 2000 Correspondence effects with manual gestures and postures: a study of imitation. *J. Exp. Psychol. Hum. Percept. Perform.* **26**, 1746–1759. (doi:10.1037/0096-1523.26.6.1746)
- Tennie, C., Call, J. & Tomasello, M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364**, 2405–2415. (doi:10.1098/rstb.2009.0052)
- Tessari, A. & Rumiati, R. I. 2004 The strategic control of multiple routes in imitation of actions. *J. Exp. Psychol. Hum. Percept. Perform.* **30**, 1107–1116. (doi:10.1037/0096-1523.30.6.1107)
- Thorndike, E. L. 1898 Animal intelligence: an experimental study of the associative processes in animals. *Psych. Rev. Mono. Suppl.* **2**, 1–8.
- Tomasello, M. 1996 Do apes ape? In *Social learning in animals: the roots of culture* (eds C. M. Heyes & B. G. Galef), pp. 319–346. London, UK: Academic Press.
- van Baaren, R., Janssen, L., Chartrand, T. L. & Dijksterhuis, A. 2009 Where is the love? The social aspects of mimicry. *Phil. Trans. R. Soc. B* **364**, 2381–2389. (doi:10.1098/rstb.2009.0057)
- Voelkl, B. & Huber, L. 2007 Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* **2**, e611. (doi:10.1371/journal.pone.0000611)
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
- Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. M. 2009 Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364**, 2417–2428. (doi:10.1098/rstb.2009.0069)