

Review

Watch and Learn: The Cognitive Neuroscience of Learning from Others' Actions

Richard Ramsey ^{1,4,*} David M. Kaplan ² and Emily S. Cross ^{2,3,4,*}

The mirror neuron system has dominated understanding of observational learning from a cognitive neuroscience perspective. Our review highlights the value of observational learning frameworks that integrate a more diverse and distributed set of cognitive and brain systems, including those implicated in sensorimotor transformations, as well as in more general processes such as executive control, reward, and social cognition. We argue that understanding how observational learning occurs in the real world will require neuroscientific frameworks that consider how visuomotor processes interface with more general aspects of cognition, as well as how learning context and action complexity shape mechanisms supporting learning from watching others.

Learning from Watching Others Is a Fundamental Human Skill

Whether learning to dance Gangnam Style, open a bottle of champagne, or tie shoelaces, humans learn a great deal by simply watching others [1,2]. Learning by observation can have many benefits over physical practice without observation. This is especially true in dangerous or novel environments where poor initial performance can be costly, such as learning to drop in on a skateboard ramp without first watching someone else do it successfully. Equally, learning by watching others is beneficial in social situations where active participation is not possible, such as watching your supervisor give critical feedback to a colleague. As such, observational learning has been of considerable interest to experts from a variety of disciplines, including social and developmental psychology, sport and exercise science, comparative biology and robotics, where researchers are examining how we learn from watching others across a range of behaviors, from simple motor movements to complex social interactions [1,3–5].

Contemporary empirical study into how we learn from watching others originated, to a large extent, in the **social learning** (see [Glossary](#)) research of Albert Bandura and colleagues starting in the 1960s [3,6–8]. Much of this early work focused on the role of an observer's motivation to learn and social factors relevant to the model. Over the past several decades, however, empirical interest in examining observational learning has come increasingly from the action domain, with considerable attention from cognitive neuroscientists who have begun to explore and characterize the systems within the human brain that translate visual signals into motor output [2,9–12]. While tremendous progress has been made in identifying the neural correlates supporting observational learning of others' actions, our understanding of how we learn from watching the actions of others remains in its infancy. The foundational structure of relevant cognitive and brain systems remains largely unknown and many key questions still need to be addressed. By synthesizing initial findings from several relevant subdisciplines of human neuroscience and placing them within a wider context of observational learning across species and agents, we aim to provide an overview of the progress that has been made towards understanding brain-based mechanisms that support observational learning. We also outline important next steps that, if taken, could generate a more complete understanding of this ubiquitous and vital capacity.

Highlights

Understanding how the human brain translates visual information into skilled motor performance has been assisted and constrained by the discovery of mirror neurons.

Emerging evidence highlights how observational motor learning involves a far more diffuse network of brain regions and cognitive processes, which are shaped by the context and complexity of the motor task to be learned.

A greater emphasis on combining functional decomposition and functional integration approaches should facilitate paradigm and discoveries that move us closer toward understanding how we learn from watching others in complex, real-world scenarios.

¹Department of Psychology, Macquarie University, Sydney, Australia

²Department of Cognitive Science, Perception in Action Research Centre, Centre for Elite Performance, Expertise, and Training, Macquarie University, Sydney, Australia

³Institute of Neuroscience and Psychology, University of Glasgow, Glasgow, Scotland

⁴These authors contributed equally

*Correspondence:
Richard.ramsey@mq.edu.au
(R. Ramsey) and
Emily.cross@mq.edu.au (E.S. Cross).



The Value of a Holistic Approach to Studying Observational Learning

Much like human neuroscience research in general, observational learning research within cognitive neuroscience has tended to focus on understanding the role of a restricted set of brain areas, such as the human **mirror neuron system**. This focus has undoubtedly contributed to our knowledge about how we learn from watching others, but it has also come at the expense of understanding and appreciating the roles played by a wider set of systems, as well as how such systems interact. These additional systems include the motor system more generally, as well as regions associated with semantic processing, attention, and memory. What is currently lacking, therefore, are frameworks describing how the brain enables information to be incorporated across distributed neural networks, some of which may be particularly relevant for action learning and others that may support a host of more general cognitive processes. Human social life is simply too complex to understand by focusing exclusively on the operation of subsystems in isolation. For example, if a clear understanding of motor development in children or expertise in dancers and athletes is to be developed, it is vital to study more than a restricted set of motor skills suitable for laboratory study (such as key pressing or moving a manipulandum), where the focus is on a subset of component systems. Likewise, if socially harmonious robotic agents that learn from and adapt to human actions are to be developed, this will require a fuller understanding not only of how skills are acquired by observation but also how they fit with other states and processes such as motivation, goals, and intentions. Without incorporating these perspectives, one is likely to fall short of a holistic understanding of the processes and systems that support observational learning in the human brain, how these develop and change across the lifespan, and how these might be modeled in artificial agents.

Given the varieties of observational learning that have been studied to date (Box 1), it is important to establish the scope of this review. We focus on a specific type of observational learning – namely observational motor learning, where action observation leads to an enduring refinement to motor performance. We have organized the review into three main parts. First, owing to its

Box 1. Varieties of Observational Learning

Multiple types of observational learning exist and, like many subdomains of cognitive neuroscience, the use of vague terminology fuels confusion and hinders progress [107,108]. We define here the specific type of observational learning that we focus on to distinguish it from related, but distinct, interests. Our aim is to provide operational definitions and distinctions that are important for this article's discussions, and we recognize that strict definitions of broad consensus may be beyond reach, given the complexity of the topic.

At its broadest, observational learning can be conceived as any instance where one observes someone and learns something new or modifies a previously learned skill or behavior. We define learning here as an enduring change in the way that an organism responds, based on its experiences [109]. In this review we focus on a subtype of observational learning that has two necessary requirements: (i) an action must be observed, and (ii) an enduring change to motor performance must occur. Several implications follow from this operational definition. First, one can study the cognitive and brain mechanisms associated with action observation without studying learning [17–19,26,110,111]. Indeed, one's ability to perform a triple Axel jump may remain unchanged after watching figure skating in the Olympic Games. Second, learning from observing actions is not the same as imitation, although they may co-occur and do rely on partly shared cognitive and brain processes. To qualify as imitation, one must copy someone, whether intentionally or not [112–114]. By contrast, one need not immediately imitate someone to learn by observation. For example, one could watch Beyoncé dancing in a music video (without copying her actions at the time) and then be better at reproducing those dance moves the following weekend when dancing in a club. Third, we can distinguish skill learning through observation of other people's actions from other forms of learning based on watching other people behave more generally, which are collectively referred to as social learning [4,115,116]. Although observational motor learning is one type of social learning, social learning also encompasses a much broader range of behaviors, some of which are extremely complex, such as how to resist peer pressure to partake in risky behaviors, respond to criticism, or interact appropriately with people from different cultures. Fourth, demonstration that particular cognitive and brain processes support observational learning does not imply that they are uniquely tied to observational learning *per se*. For example, given the links between motor imagery and action observation [117–119], it is possible that processes common to motor imagery and action observation are involved to some extent when learning by watching others.

Glossary

Functional near-infrared spectroscopy (fNIRS): a human neuroimaging modality which, like fMRI, maps the blood oxygen level-dependent response and takes advantage of the transparency of biological tissue (such as skin and bone) to the near-infrared spectrum. Light shone on the head with laser diodes travels through the skull and scatters back in a banana-shaped curve, and is eventually picked up by a detector located ~3 cm away from the light source. fNIRS has a relatively shallow penetration depth (only reaching the outer layers of the cerebral cortex), as well as relatively low spatial (2–3 cm) and temporal (up to 10 Hz) resolution. Although its spatial resolution is lower than fMRI and its temporal resolution is slower than electroencephalography (EEG), fNIRS brings other advantages to researchers in terms of cost efficacy, portability, and its relative robustness to movement artefacts.

Mirror neuron system: also referred to as the core mirror neuron system, regions of inferior frontal gyrus/ventral premotor cortex and inferior parietal lobule in the human brain that show similar responses to observed and performed actions. These regions of cortex are the human homologs of the brain regions where mirror neurons were originally discovered within the macaque non-human primate brain (F5 and IPL).

Mirror neurons: a class of neurons originally identified in the non-human primate premotor cortex that discharge when a monkey performs an action or observes another monkey or human perform the same action.

Motor adaptation: a type of error-driven motor learning process that leads to the acquisition or recalibration of movement patterns suited to a specific context or environment (such as when operating in a force field, reaching under variable loads, or hitting a golf ball on a windy day).

Repetitive transcranial magnetic stimulation (rTMS): a noninvasive neurostimulation technique in which electromagnetic pulses are applied in rapid succession by a coil placed on the scalp, above a cortical region of interest. The stimulation provides a temporary disruption to the processing of neurons located in the patch of cortex directly beneath the coil, known as a virtual lesion.

dominance, we review research into the role of the human mirror neuron system in observational learning. Next, we review evidence implicating motor processes extending beyond the mirror system in observational learning. We outline how research on sequence learning and **motor adaptation** in particular informs our understanding of the neural substrates underlying observational learning. Finally, we review evidence highlighting the roles played by non-motor systems in observational learning, such as those associated with cognitive control and reward. We also detail how systems or frameworks that might seem less relevant to understanding observational learning, such as semantic and memory systems, as well as 'real-life' neuroscience approaches, also hold considerable potential for making progress in this endeavor.

We conclude by articulating what is known and what remains to be discovered regarding the cognitive neuroscience of learning from watching others. If the ultimate goal is to understand observational learning as it occurs in daily life, there is a need to consider a distributed and diverse set of interacting neurocognitive systems both within and beyond the human mirror neuron system. It is also imperative to combine evidence gathered from controlled laboratory conditions with work that puts observational learning to the test in complex and rich real-world contexts to better understand how to support and bolster this vital skill.

The Dominance of the Human Mirror Neuron System in Cognitive Neuroscience Investigations of Observational Learning

Cognitive neuroscientific investigations into observational learning have focused extensively on the role played by the human mirror neuron system (Box 2). Since the discovery of **mirror neurons** within premotor and, later, inferior parietal cortices of the non-human primate brain [13–15], researchers have sought to determine whether similar neural processes exist within the human brain. To do so, researchers have used a variety of noninvasive neuroimaging and neurostimulation

Serial reaction time (SRT) task: an often-used task in motor learning research to study implicit learning, where participants are asked to continually respond to a fixed set of cues, where each cue signifies a specific response to be made, such as a button press.

Social learning: the process through which new behaviors are learned by watching and imitating others.

Box 2. Charting the Core and Extended Mirror Neuron Systems

In the human mirror neuron system literature, most studies relate to activity within inferior parietal and ventral premotor cortices in the human brain [120]. These cortices represent the human homologs of rhesus macaque monkey brain regions where mirror neurons were first discovered [13,121]. Neurons within macaque ventral premotor and inferior parietal cortices were found to respond to the observation and execution of hand and mouth actions, and early neuroimaging work performed with human participants also found spatial overlap within ventral premotor and inferior parietal cortices when people observed or executed movements [16,122–124].

Since the initial discoveries of mirror neurons in monkeys, and follow-up work with humans, several other human brain regions have been reported to show similar mirror-like properties, including the insula and anterior mesial frontal cortex (together referred to as the limbic mirror system, thought to be involved in the recognition of affective behavior [125]), primary motor cortex [126], dorsal premotor cortex, superior parietal lobule, cerebellum [18], supplementary motor area, and the medial temporal lobe [127]. Concurrent with a growing number of brain areas reported to respond during the perception and production of certain behaviors came a proliferation of proposals for the behaviors and psychological tasks that such an extended mirror neuron system might drive [37]. These span diverse topics including language, general learning, autism, mind reading, and imitation, among others. In an attempt to incorporate this expanding cartography of neural tissue demonstrating mirror-like properties into our understanding of mirror neurons based on the original discovery, some authors have argued that, instead of focusing on a core or extended mirror neuron systems *per se*, it is more productive to think about mirroring mechanisms distributed throughout the brain, and which link visual representations of others' behavior into one's own visceromotor representations based on the relevant domain [110].

In this review we draw particular attention to the dominant role played by the core mirror system in observational learning research. Partly owing to the primacy of discovery of mirror properties within these regions, frontoparietal mirror activity has received the most attention across a variety of domains, including observational learning. However, although precedence of discovery matters on a practical level, it is important to keep in mind that such precedence can also lead the research community to artificially privilege certain brain regions above others, even if these rankings may not directly relate to the actual ways the human brain works. As we argue in this review, the key role played by extended mirror system regions (as well as non-mirror brain regions) in observational learning illustrates the importance of considering interplay between distributed brain circuits when studying any complex form of cognition.

measures to probe links between action and perception [16–22]. This work revealed compelling evidence that the human mirror neuron system is engaged not only during action perception and performance but is also sensitive to learning and experience, with more familiar actions leading to more robust engagement [23–26]. Furthermore, research examining learning guitar chords [27–29], dance movements [9,30], and assembling or using novel objects [10,31–33] reported converging evidence that frontoparietal brain regions are modulated when observation of others' actions resulted in subsequent learning. This evidence has led to a general understanding within cognitive neuroscience that action learning by observation relies, at least in part, on functions performed by the mirror neuron system.

A role for the human mirror neuron system in observational learning makes intuitive sense, given that the neurons found in these cortical regions have well-documented sensory and motor properties. At the same time, we argue that an outsized focus on the human mirror neuron system has produced an oversimplified account of the neural underpinnings of observational learning. Indeed, as already foreshadowed in an early meta-analysis [16], as well as more recent empirical work (e.g., [28,34–36]), several lines of evidence document brain regions and systems extending beyond the mirror neuron system that contribute to this fundamental capacity. In the following sections we examine the role(s) played by some of these systems. Our starting point is that the mirror neuron system is unlikely to be the 'center' of any complex cognitive process. Instead, we argue that the mirror neuron system is likely to perform a range of different subprocesses that contribute to many broader cognitive functions [37]. Consequently, we offer a deflationary account of the mirror neuron system in observational learning, which assigns a more limited role to this system than is typically proposed. Instead of the mirror system being the star (or even solo) performer in observational learning, we emphasize how this type of learning is far more likely to rely on coordinated interplay between the mirror neuron system and other brain networks.

The Role of an Extended Motor Network in Observational Learning

In this section we review recent work on observational motor learning highlighting roles for cognitive and brain systems extending beyond the core brain regions traditionally associated with the mirror neuron system. We focus on two broad types of task: sequencing learning and motor adaptation [38] (Box 3). Studying sequence learning holds value because, in real life, much of skilled human behavior follows a sequential structure (e.g., learning to speak, dance, play the piano, ride a bike, and drive a car). Moreover, like many other kinds of human behavior, sequence learning can be achieved via physical practice or by observing others [2]. Observational motor sequence learning is often studied via the **serial reaction time (SRT)** task (Box 3), and shares two important behavioral characteristics with motor learning achieved primarily through physical practice. First, increasing the number of observation trials improves learning in much the same manner as increasing the number of physical practice trials does [39]. Second, contextual interference effects occur in observational settings [40] exactly as they do in physical practice settings [41–43]. Therefore, learning via physical and observational practice appears to rely on partially shared cognitive foundations [1,2,44–46].

To date, a small but growing number of functional magnetic resonance imaging (fMRI) studies have investigated the neural substrates underpinning observational motor sequence learning. Some researchers have used tasks involving learning the correct sequence of movements to assemble an object [31]. When watching the sequence of actions with the intention to learn compared with a perceptual control task, widespread engagement emerged across inferior and superior frontal and parietal cortices, presupplementary motor area (pre-SMA), the cerebellum, basal ganglia, and the hippocampus. Likewise, others have used dance and complex knot-tying paradigms to study observational sequence learning [9,10]. These studies show that

Box 3. Key Paradigms for Studying Motor Learning in Visual and Physical Domains

Motor Sequence Learning

Motor sequence learning refers to the process by which a sequence of movements comes to be executed with increasing speed, accuracy, and precision over time [128]. Observational motor sequence learning describes how movement sequences (i.e., motor skills) can be acquired by observing the actions of others. This type of learning has been reported in tool manipulation [7], knot-tying [10], dance [129], relative timing [45], and serial reaction time (SRT) tasks [130–132]. On each trial in a standard SRT task, a visual stimulus appears on the screen at one of several locations and participants must select the appropriate response button as quickly as possible (Figure 1A). Visual stimuli are either presented in a predictable, repeating sequence or at random. Learning is indicated by a steady decrease in response time during a block of sequential trials, and a pronounced increase in response time for a random trial following a sequential block.

Visuomotor Adaptation

Whereas motor sequence learning supports the acquisition of complex motor skills, motor adaptation supports the maintenance of consistent performance in response to bodily or environmental changes. Consider the role of motor adaptation in golf. The outcome of every golf swing depends not only on intrinsic properties of the player’s swing but also on fluctuations in the external environment such as the wind and temperature. Professional golfers sense and adapt their swings to compensate for these external perturbations so that they can consistently hit accurate shots. Motor adaptation is generally important for humans because our bodies and environments continually change over multiple timescales, which alters the mapping from motor command to behavioral outcome. For instance, when muscles fatigue or limb dynamics change as a result of growth during development, the same motor commands will no longer lead to the same outcome. Motor adaptation recalibrates this mapping so that stable performance can be maintained.

Motor adaptation is frequently studied using visuomotor adaptation tasks. In a typical visuomotor adaptation paradigm, participants perform simple reaching movements using perturbed visual feedback [38]. This is commonly done by changing the relationship between the position of the hand and the position of an on-screen cursor. For example, in visuomotor rotation experiments, cursor feedback is rotated clockwise or counterclockwise about the starting position by x (e.g., 30°) so that, for the cursor to move directly toward the target, the participant would need to reach x degrees in the opposite direction of the cursor rotation. This novel visuomotor mapping between movements and the sensory consequences of those movements (i.e., visual feedback) results in initial reaching errors which the motor system uses to gradually adjust future movements until reaching becomes accurate once again (Figure 1B).

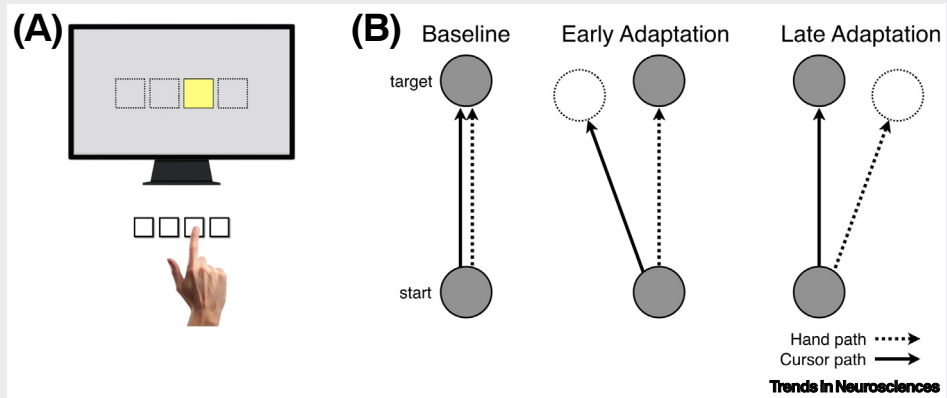
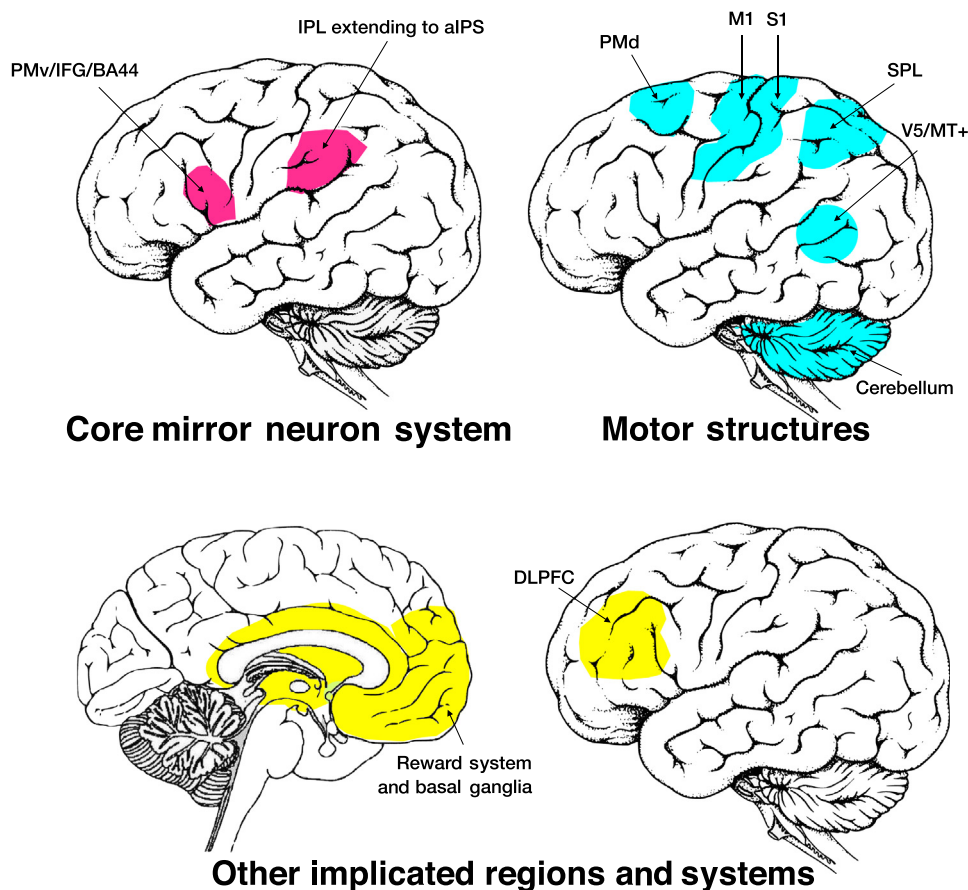


Figure 1. Key Paradigms for Studying Observational Motor Learning. (A) Serial reaction time (SRT) task. (B) Visuomotor adaptation task, adapted from [133].

when people watch dance sequences they learned via observation, or view pictures of knots that they observed another person learn to tie, dorsal premotor cortex shows stronger engagement compared with observing untrained stimuli. In addition, several fMRI studies have used the SRT task to probe the neural correlates of observational learning [11,28,36,47]. Across these studies, researchers consistently report sensitivity within dorsal premotor cortex and superior parietal lobule, as well as ventral premotor cortex, when learning SRT tasks via observation. These results show that observational motor sequence learning is not restricted to engagement of inferior frontal and parietal brain regions but extends to a broader motor network that includes dorsal premotor, superior parietal, and cerebellar regions (Figure 1).

Brain imaging research on the motor system also highlights how responses can increase or decrease following learning, depending on a range of factors, which can complicate the interpretation of learning-related neural activity changes. Activation decreases following both physical and observational sequence learning have been reported in inferior and superior portions of the anterior parietal lobe, as well as in ventral and dorsal premotor cortex [11,28,36,48]. This is consistent with a general pattern reported in the literature of activity decreases across a number of areas, including primary motor cortex (M1), pre-SMA, and dorsolateral prefrontal cortex (DLPFC), during the initial fast stages of learning a sequential motor task (reviewed in [49]). Importantly, later stages of learning are associated with activation increases in M1, SMA, ventral premotor cortex (PMv), and primary somatosensory cortex (S1) ([50,51], reviewed in [49]; cf [52] for a contrasting view). Whether observational motor sequence learning occurring over even longer time-periods (months and years rather than weeks and days) results in similar increases in activation in areas that exhibited short-term learning-related decreases remains unexplored.



Trends in Neurosciences

Figure 1. Human Brain Regions Implicated in Observational Motor Learning. Many studies to date that have examined observational motor learning have focused on the core mirror neuron system, but emerging evidence suggests vital contributions are also made by several other motor areas, as well as by brain systems implicated in reward, executive control, and memory. Further discussion of the relationship between the core and extended mirror neuron system is given in [Box 2](#). Abbreviations: aIPS, anterior intraparietal sulcus; BA44, Brodmann area 44; DLPFC, dorsolateral prefrontal cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; M1, primary motor cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; S1, primary somatosensory cortex; SPL, superior parietal lobule; V5/MT+, middle temporal visual area. Brain schematics accessed from [Needpix.com](#).

Whereas motor sequence learning supports the acquisition of complex motor skills, motor adaptation supports the maintenance of consistent performance in response to changes in the body or external environment (Box 3). According to the dominant theoretical framework, this type of learning involves the recalibration of internal models (i.e., representations of body–environment interactions) used to support feedforward and feedback motor control [53–56]). Observational motor adaptation describes how individuals can learn to respond to novel sensorimotor perturbations by observing someone else adapt their movements to those same perturbations. Observation has been shown to facilitate visuomotor adaptation [46–48], force-field adaptation [46,57,58], and force estimation [59,60]. For example, in experiments probing the effects of observation on subsequent visuomotor adaptation [61–63], participants observe someone else learning to reach using rotated visual feedback. When observers are subsequently exposed to the same visuomotor rotation, their reaches become more accurate during initial exposure compared with those who had no previous observational experience.

Despite their similarities, some important differences have also been noted between observational and first-hand, physical visuomotor learning. First, although passive observers exhibit improved learning when they encounter the same visuomotor perturbation they previously observed, they do not show after-effects (reaching errors in the normal unperturbed environment following exposure to perturbed conditions) – a hallmark of implicit motor adaptation [61,62]. Second, observers do not suffer interference costs when consecutively learning two opposing visuomotor perturbations, another defining characteristic of implicit motor adaptation [64,65]. These results imply that the benefits of observation may reflect learning explicit aiming strategies [66] as opposed to using motor errors on a trial-by-trial basis to incrementally update an internal model [67–69]. More work is needed in this area to identify the underlying mechanisms.

Examining the neural mechanisms underlying observational learning using motor adaptation tasks is a growing area of research, and novel insights are coming from studies employing neurostimulation and neuroimaging methods. In one study, **repetitive transcranial magnetic stimulation (rTMS)** was applied over M1 after participants observed someone learning to reach in a force field [70]. Even though observation improved subsequent learning in a control group, participants in the rTMS group showed degraded adaptation to the same force field they observed at levels comparable with another group of controls who received no observational experience at all. Similarly, single-pulse TMS over M1 has been shown to induce larger increases in corticospinal excitability when observing motor learning compared with observing similar movements that involved no learning [71]. In addition to M1, emerging evidence supports a tight interplay between sensory and motor areas during motor learning by observing [72,73]. For example, a role for S1 in observational learning in motor adaptation tasks has been demonstrated using median nerve stimulation to disrupt the function of S1 [35]. Stimulation delivered to the same arm used in the observed action impaired subsequent learning, whereas stimulation of the opposite arm did not. Together, results from neurostimulation studies indicate a crucial role for M1 and S1 in learning by observation.

Neural reorganization following observational learning has also been studied using fMRI combined with motor adaptation tasks. For example, in a study where participants observed movement errors performed when adapting to novel force fields [57], the authors found activation of portions of the posterior parietal cortex, dorsal premotor cortex, and cerebellum. In another fMRI study [58] the authors investigated changes in resting-state functional connectivity after participants observed others complete a force-field learning task and identified a network consisting

of the middle temporal visual area (V5/MT), S1, M1, and cerebellum. Importantly, connectivity changes correlated with the amount of learning gained through observation. Subsequent work showed that individual differences in pretraining resting-state functional connectivity in sensorimotor brain areas could predict the amount of learning by observation [74]. The studies reviewed in this section demonstrate that, even if one only considers standard motor learning paradigms, a widespread and distributed neural network is involved when learning from watching other people's actions. Accordingly, even simple, pared-down tasks involving relatively simple actions (e.g., planar reaching, button pressing, etc.) recruit a complex network of brain areas that extends beyond the mirror neuron system (Figure 1). These considerations underscore the value to be gained from broadening the focus of observational learning research.

The Role of Non-motor Systems and Frameworks

Brain circuits beyond the motor system have received less attention in the context of observational motor learning. This makes sense, given that the motor system is the obvious place to start when attempting to understand the brain mechanisms that underpin motor skill learning (observational or otherwise). However, as outlined earlier, to scientifically understand complex processes or systems, one must consider how the component subprocesses or subsystems operate both in isolation and in combination [75,76]. In addition, one of the earliest and arguably most influential psychological theories of observational learning to date emphasized that a wide range of non-motor factors, such as an individual's motivation to learn, also make important contributions to observational learning [3]. In this section we review research implicating a role for non-motor systems in observational learning, including those associated with cognitive control and reward. We also outline how considerable value should be gained from exploring observational learning from different perspectives, such as those associated with semantic or memory systems and so-called 'real-life' neuroscience approaches. Finally, we suggest that observational learning is a prime case where 'neuroscience needs behavior' [77]. In other words, our understanding of how brain systems support observational learning will be fundamentally limited until neuroscientific methods can be connected to real-world behavior in meaningful ways.

The first two perspectives that we consider have already been studied in observational learning contexts, albeit to a relatively small degree. The first concerns general cognitive control processes, which are reliably associated with bilateral DLPFC [78,79]. Cognitive control processes regulate other mental processes and guide attention onto relevant features of the environment through processes such as alerting, orienting, filtering, and inhibition [80]. The versatility of this frontoparietal brain network to operate across a range of tasks and contexts has led to it being labeled the 'multiple demand network' [79]. In the context of observational learning, depending on the type of learning task or aims of the individual, cognitive control is necessary to direct attention to features that are most relevant in a given context. The efficiency and effectiveness of such control processes also likely contributes to the observational learning rate. Indeed, evidence has shown that DLPFC correlates with performance gains following with observational practice of a guitar chord learning task [28]. Furthermore, transcranial magnetic stimulation to DLPFC makes behavior more error-prone when performing motor sequences previously learned via observation, but not through physical practice [81]. As such, visual and motor processes do not appear to operate in isolation, but are instead modulated by other task demands, which are likely to reflect a range of other supervisory and control processes.

The second system concerns reward and value-based learning [34,134,135]. For example, some authors have made the case that basic principles of learning, such as those grounded in Pavlovian and instrumental learning, must be considered together with advances in social cognition to

better understand observational learning [34]. Across a range of non-human species, they show that social learning is partly indexed by similar reward centers in the brain that coordinate learning by direct experience. Similarly, in humans, single-neuron recordings have identified neurons in the amygdala that track the expected value of any given trial in a gambling task based on one's own experience, as well as knowledge gained from watching others [82]. Accordingly, it has been suggested that learning from others is partly mediated by a general-purpose value system in combination with more socially specific processes such as mental state reasoning [34]. Future research building on these value processes and extending them more deeply into the domain of human neuroscience would be particularly valuable, especially given that a strong foundation exists in the non-human literature to guide predictions.

In addition to cognitive control and reward processes, it is also important to consider perspectives that have not yet been widely considered in cognitive neuroscience models of observational learning. Consider semantic cognition research, for instance, which investigates how meaning is extracted from interactions with the environment (e.g., [83,84]). This perspective has recently been applied to social cognition more generally, under the view that observing other people is nothing special and is merely one more way to learn about the world and people in it [85]. Another example is research on memory systems. Recent theoretical work makes the case for how research on impression formation, which is a form of learning about people and their trait characteristics, could benefit from a much greater consideration of developments in the neuroscience of memory [86]. The proposal outlines how distinct types of memory, such as episodic, associative, and instrumental, are associated with distinct but interacting brain circuits, and such knowledge is likely to inform how social aspects of knowledge are stored and retrieved. We would argue that the same lessons apply to research on observational learning. Specifically, important questions to explore include which types of memory systems are involved when we learn from watching others, how the learning or social context shapes their engagement, and how they interface with social information processing systems more generally. One major advantage of considering semantic and memory frameworks in more depth is that they are based on decades of research across multiple species, thus providing a rich foundation to build upon.

Finally, we offer two further proposals. First, to accelerate progress toward understanding how we learn from others in daily life, it will be important to consider the fast-changing developments that are emerging in 'real-life' neuroscience [87–89,136]. For instance, how do individuals learn from other people when interacting in groups? How do complex contextual signals, such as person identity, type of action, and setting (e.g., exam conditions, combat, surgery, or leisure time) interfere with or facilitate observational motor learning? Although some laboratory work has taken steps toward understanding action learning among dyads present in a laboratory (as opposed to watching video-based representations of to-be-learned actions; e.g., [10]), current understanding of how learning unfolds in complex real-world contexts where multiple models and environmental pressures and opportunities are present remains limited at the behavioral (let alone neural) level. This progress will require the development of approaches that work both within and beyond the confines of the research laboratory. Portable neuroscience technologies, such as **functional near-infrared spectroscopy (fNIRS)**, may offer a suitable methodological approach to bridge this gap between the research laboratory and the real world [90–92]. Embracing more 'real-life' neuroscience approaches will likely further reinforce the need to take an expanded view of the cognitive and brain systems involved in observational learning. A fuller understanding of how we learn from others in daily life stands to further advance several related areas of inquiry, including motor development and learning across the lifespan, how expertise is established, and how best to program robots to accomplish joint actions with human users.

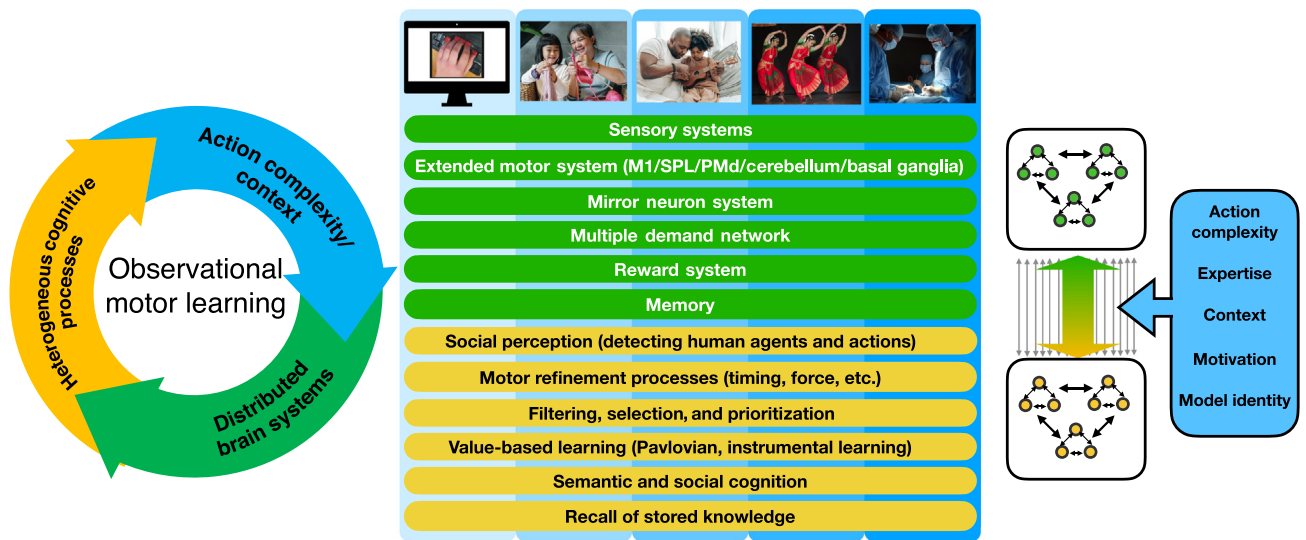
Second, much like neuroscience research more generally, the role of behavior in revealing principles of observational learning should not be undervalued [77]. For instance, in a laboratory sequence-learning task, behavioral research has shown that individual differences in dimensions of personality, working memory, and intelligence play a minimal role in observational learning [93]. Such findings may help to constrain expectations about the underlying brain mechanisms, especially those that may be more or less variable across individuals. That said, while behavioral experiments are certainly crucial for understanding the phenomenon of observational learning, we advocate a pluralistic approach in which investigations across multiple levels of description can play complementary roles in elucidating the links between brain and behavior [77,94–96]. It is becoming increasingly clear that both behavioral and neural data can help to adjudicate between competing mechanistic models and place useful constraints on mechanism discovery in the human brain [97,98].

Overall, our central argument in this section is that, for more substantial progress to be made, we encourage the field to fully embrace research perspectives from separate but related domains. Progress will be facilitated by a greater focus on generalized processes and other general frameworks, which are not necessarily or strictly tied to visual or motor processing *per se* [99–102].

Key Figure

Towards an Expanded Framework of Studying Observational Motor Learning

The mapping between brain systems and cognitive processes is likely complex and ‘many-to-many’ in structure



Trends In Neurosciences

Figure 2. An updated account of observational motor learning requires concurrent consideration of the role played by distributed brain systems, heterogeneous cognitive processes, and the complexity and context of any given action to be learned. Illustrated in the figure are some possible brain systems (in green) and cognitive processes (in yellow) that are likely to be involved to a greater or lesser extent when we learn from watching others’ actions, depending on the complexity, expertise of the performer and observer, learning context, learner’s motivation, and the model’s identity (in blue). This heuristic is not intended to be exhaustive or prescriptive, and instead suggests some of the contextual, neural, and cognitive features that are likely to shape observational motor learning. We stress that this is a call towards a general approach or framework for studying observational learning, which currently lacks specificity. Indeed, at this point in the development of the framework, we are simply trying to put together a broader set of processes and brain networks than has previously been considered in the context of observational learning. For reasons outlined in the main text, this is an important first step towards firmer progress. However, we acknowledge no hierarchy or prioritization in the proposal – that is, we expect all aspects to be involved to some degree because observational learning is likely to reflect complex, interacting cognitive and brain processes (like all forms of complex cognition). Image sources of the five photographs in middle panel: respectively the authors, Alex Green from Pexels, Ketut Subiyanto from Pexels, Kohinoor Darda, and Olga Guryanova (@designer4u) from Unsplash. Abbreviations: M1, primary motor cortex; PMd, dorsal premotor cortex; SPL, superior parietal lobule.

Concluding Remarks

Our review of the current state of knowledge on the cognitive neuroscience of observational learning raises several considerations for future research (see Outstanding Questions). Studying component processes in isolation and under controlled laboratory conditions has made valuable contributions to understanding cognitive and brain mechanisms of observational learning and will continue to do so. At the same time, an overemphasis on one system or process can give the illusion that complex and multifaceted processes can be reduced to the workings of a few solitary cognitive and brain subsystems [103,137].

Future observational learning research may benefit from taking a different starting point, which is predicated on an updated and richer set of assumptions (Figure 2, Key Figure). We suggest that it will be valuable to start from a position that expects a large number of 'many-to-many' mappings between cognitive processes and brain circuits. To better understand how we learn from others in the real world, the contributions of a multitude of factors (social, semantic, motivational, contextual) that may up- or downregulate basic observational learning processes must be considered. A consequence is that, to understand basic motor processes, one must understand how they operate in tandem with a diverse set of social goals that those actions sometimes serve. This is not to say that all research in this domain should change tack to focus exclusively on interactions between and integration across networks. Instead, going forward, a combination of functional segregation and integration perspectives will be necessary. One particular promising approach for accelerating progress toward a deeper understanding of observational motor learning is the type of neural network modeling that is gaining momentum in human motor learning research (e.g., [104–106]). A combination of methodological and theoretical expertise from a wider range of cognitive neuroscience subdisciplines should bring this field closer to characterizing how the human brain can translate information about other people's actions from observation into sound tooth-brushing technique, the intricate hand and foot moves of Bharatanatyam dance, or the ability to successfully perform minimally invasive surgery.

Acknowledgments

This review originates from observational learning projects in the Social Brain in Action laboratory supported by the Ministry of Defence of the UK Defence Science and Technology Laboratory (grant DSTLX-1000083177 to E.S.C. and R.R.) and the Economic and Social Research Council (grant ES/K001884/1 to R.R. and ES/K001892/1 to E.S.C.). The writing of this article was supported by funding from the European Research Council (ERC) under the EU Horizon 2020 research and innovation program (grant agreement 677270 to E.S.C.) and the Leverhulme Trust (PLP-2018-152 to E.S.C.).

Declaration of Interests

The authors declare no competing interests in relation to this work.

References

- Hodges, N.J. *et al.* (2007) What is modelled during observational learning? *J. Sports Sci.* 25, 531–545
- Vogt, S. and Thomaschke, R. (2007) From visuo-motor interactions to imitation learning: behavioural and brain imaging studies. *J. Sports Sci.* 25, 497–517
- Bandura, A. and Walters, R.H. (1977) *Social Learning Theory*, Vol. 1. Prentice-Hall Englewood Cliffs
- Csibra, G. and Gergely, G. (2009) Natural pedagogy. *Trends Cogn. Sci.* 13, 148–153
- Carcea, I. and Froemke, R.C. (2019) Biological mechanisms for observational learning. *Curr. Opin. Neurobiol.* 54, 178–185
- Bandura, A. and Jeffrey, R.W. (1973) Role of symbolic coding and rehearsal processes in observational learning. *J. Pers. Soc. Psychol.* 26, 122
- Carroll, W.R. and Bandura, A. (1982) The role of visual monitoring in observational learning of action patterns: making the unobservable observable. *J. Mot. Behav.* 14, 153–167
- Carroll, W.R. and Bandura, A. (1990) Representational guidance of action production in observational learning: a causal analysis. *J. Mot. Behav.* 22, 85–97
- Cross, E.S. *et al.* (2009) Sensitivity of the action observation network to physical and observational learning. *Cerebr. Cortex* 19, 315–326
- Cross, E.S. *et al.* (2017) Learning to tie the knot: the acquisition of functional object representations by physical and observational experience. *PLoS One* 12, e0185044
- Sakreida, K. *et al.* (2018) Cognitive control structures in the imitation learning of spatial sequences and rhythms – an fMRI study. *Cereb. Cortex* 28, 907–923
- Hodges, N.J. (2017) Observations on action-observation research: an autobiographical retrospective across the past two decades. *Kinesiol. Rev.* 6, 240–260
- Gallese, V. *et al.* (1996) Action recognition in the premotor cortex. *Brain* 119, 593–609

Outstanding Questions

How, when, and between which cognitive and brain systems does functional integration occur during observational learning?

How can laboratory-based research best connect to and inform real-life observational learning processes?

How best can we accommodate contributions made by the mirror neuron system to observational learning, while also remaining open and sensitive to the influence of non-mirror neuron structures and systems whose influence might be more subtle and context-specific?

Especially during the current time of pandemic-related social isolation and the consequent shift to online instruction for millions of students of all ages, to what extent can people learn complex new motor behaviors from video-based instruction alone, and what do live, embodied models contribute to learning above and beyond screen-based instruction?

How are observational learning-related increases and decreases in neural engagement related to performance and efficiency gains across time, and how do these fluctuations in engagement relate to those seen during physical practice/learning?

To what extent do the performance gains reported in existing observational motor learning studies reflect the learning of explicit cognitive strategies and heuristics versus learning that is largely implicit and automatic?

How might the contributions of different neurocognitive systems to observational learning be up- or downregulated to improve observational learning in laboratory as well as real-world contexts?

How dynamic is the interplay between different cognitive and brain systems during observational learning, and how does this interplay change throughout the lifespan? How might factors such as motor development, skill, semantic knowledge, and memory shape how we learn from others in motor and non-motor contexts, from early life through to advanced age?

14. Rizzolatti, G. *et al.* (1996) Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3, 131–141
15. Fogassi, L. *et al.* (2005) Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667
16. Grèzes, J. and Decety, J. (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum. Brain Mapp.* 12, 1–19
17. Caspers, S. *et al.* (2010) ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage* 50, 1148–1167
18. Molenberghs, P. *et al.* (2012) Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. *Neurosci. Biobehav. Rev.* 36, 341–349
19. Hardwick, R.M. *et al.* (2018) Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosci. Biobehav. Rev.* 94, 31–44
20. Fadiga, L. *et al.* (1995) Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73, 2608–2611
21. Strafella, A.P. and Paus, T. (2000) Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport* 11, 2289–2292
22. Catmur, C. *et al.* (2007) *Sensorimotor learning configures the human mirror system.* 17(17) pp. 1527–1531
23. Kilner, J.M. *et al.* (2003) An interference effect of observed biological movement on action. *Curr. Biol.* 13, 522–525
24. Buccino, G. *et al.* (2004) Neural circuits involved in the recognition of actions performed by nonconspecifics: an fMRI study. *J. Cogn. Neurosci.* 16, 114–126
25. Calvo-Merino, B. *et al.* (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr. Biol.* 16, 1905–1910
26. Cross, E.S. *et al.* (2006) Building a motor simulation de novo: observation of dance by dancers. *NeuroImage* 31, 1257–1267
27. Buccino, G. *et al.* (2004) Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 42, 323–334
28. Higuchi, S. *et al.* (2012) Imitation and observational learning of hand actions: prefrontal involvement and connectivity. *NeuroImage* 59, 1668–1683
29. Gardner, T. *et al.* (2017) Using guitar learning to probe the action observation network's response to visuomotor familiarity. *NeuroImage* 156, 174–189
30. Kirsch, L.P. and Cross, E.S. (2015) Additive routes to action learning: layering experience shapes engagement of the action observation network. *Cereb. Cortex* 25, 4799–4811
31. Frey, S.H. and Gerry, V.E. (2006) Modulation of neural activity during observational learning of actions and their sequential orders. *J. Neurosci.* 26, 13194–13201
32. Rüter, N.N. *et al.* (2014) Observed manipulation of novel tools leads to mu rhythm suppression over sensory-motor cortices. *Behav. Brain Res.* 261, 328–335
33. Rüter, N.N. *et al.* (2014) Observed manipulation enhances left fronto-parietal activations in the processing of unfamiliar tools. *PLoS One* 9, e99401
34. Olsson, A. *et al.* (2020) The neural and computational systems of social learning. *Nat. Rev. Neurosci.* 21, 197–212
35. McGregor, H.R. *et al.* (2016) Functional plasticity in somatosensory cortex supports motor learning by observing. *Curr. Biol.* 26, 921–927
36. Apšvalka, D. *et al.* (2018) Observing action sequences elicits sequence-specific neural representations in frontoparietal brain regions. *J. Neurosci.* 38, 10114–10128
37. Heyes, C. and Catmur, C. (2020) What happened to mirror neurons? *PsyArXiv* Published online July 8, 2020. <http://dx.doi.org/10.31234/osf.io/dtnqg>
38. Krakauer, J.W. *et al.* (2019) Motor learning. *Compr. Physiol.* 9, 613–663
39. Blandin, Y. and Proteau, L. (1997) On the cognitive processes involved in the contextual interference effect. *J. Hum. Mov. Stud.* 32, 211–233
40. Blandin, Y. *et al.* (1994) On the cognitive processes underlying contextual interference and observational learning. *J. Mot. Behav.* 26, 18–26
41. Lee, T.D. and Magill, R.A. (1983) The locus of contextual interference in motor-skill acquisition. *Journal of Experimental Psychology: Learning, Mem. Cogn.* 9, 730
42. Shea, J.B. and Morgan, R.L. (1979) Contextual interference effects on the acquisition, retention, and transfer of a motor skill. *J. Exp. Psychol. Hum. Learn. Mem.* 5, 179
43. Cross, E.S. *et al.* (2007) Neural substrates of contextual interference during motor learning support a model of active preparation. *J. Cogn. Neurosci.* 19, 1854–1871
44. Boutin, A. *et al.* (2010) Role of action observation and action in sequence learning and coding. *Acta Psychol.* 135, 240–251
45. Blandin, Y. *et al.* (1999) Cognitive processes underlying observational learning of motor skills. *Q. J. Exp. Psychol. Sect. A* 52, 957–979
46. Mattar, A.A.G. and Gribble, P.L. (2005) Motor learning by observing. *Neuron* 46, 153–160
47. van der Helden, J. *et al.* (2011) Observational learning of new movement sequences is reflected in fronto-parietal coherence. *PLoS ONE* 5, e14482
48. Wiestler, T. *et al.* (2013) Skill learning strengthens cortical representations of motor sequences. *Elife* 2, e00801
49. Dayan, E. and Cohen, L.G. (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72, 443–454
50. Steele, C.J. and Penhune, V.B. (2010) Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *J. Neurosci.* 30, 8332–8341
51. Wymbs, N.F. and Grafton, S.T. (2015) The human motor system supports sequence-specific representations over multiple training-dependent timescales. *Cereb. Cortex* 25, 4213–4225
52. Berlot, E. *et al.* (2020) A critical re-evaluation of fMRI signatures of motor sequence learning. *Elife* 9, e55241
53. McNamee, D. and Wolpert, D.M. (2019) Internal models in biological control. *Annu. Rev. Control Robot. Auton. Syst.* 2, 339–364
54. Wolpert, D.M. *et al.* (1995) An internal model for sensorimotor integration. *Science* 269, 1880–1882
55. Miall, C. and Wolpert, D.M. (1996) Forward models for physiological motor control. *Neural Netw.* 9, 1265–1279
56. Wolpert, D.M. *et al.* (1998) Internal models in the cerebellum. *Trends Cogn. Sci.* 2, 338–347
57. Wanda, P.A. *et al.* (2013) State dependence of adaptation of force output following movement observation. *J. Neurophysiol.* 110, 1246–1256
58. Williams, A. and Gribble, P.L. (2012) Observed effector-independent motor learning by observing. *J. Neurophysiol.* 107, 1564–1570
59. Reichelt, A.F. *et al.* (2013) Adaptation of lift forces in object manipulation through action observation. *Exp. Brain Res.* 228, 221–234
60. Buckingham, G. *et al.* (2014) Observing object lifting errors modulates cortico-spinal excitability and improves object lifting performance. *Cortex* 50, 115–124
61. Lim, S.B. *et al.* (2014) Manipulating visual-motor experience to probe for observation-induced after-effects in adaptation learning. *Exp. Brain Res.* 232, 789–802
62. Ong, N.T. and Hodges, N.J. (2010) Absence of after-effects for observers after watching a visuomotor adaptation. *Exp. Brain Res.* 205, 325–334
63. Ong, N.T. *et al.* (2012) In the absence of physical practice, observation and imagery do not result in updating of internal models for aiming. *Exp. Brain Res.* 218, 9–19
64. Krakauer, J.W. *et al.* (2005) Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neurosci.* 25, 473–478
65. Wigmore, V. *et al.* (2002) Visuomotor rotations of varying size and direction compete for a single internal model in a motor working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 28, 447
66. McDougle, S.D. *et al.* (2016) Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends Cogn. Sci.* 20, 535–544
67. Tseng, Y-w. *et al.* (2007) Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J. Neurophysiol.* 98, 54–62
68. Izawa, J. *et al.* (2012) Cerebellar contributions to reach adaptation and learning sensory consequences of action. *J. Neurosci.* 32, 4230–4239

69. Herzfeld, D.J. *et al.* (2018) Encoding of error and learning to correct that error by the Purkinje cells of the cerebellum. *Nat. Neurosci.* 21, 736–743
70. Brown, L.E. *et al.* (2009) Repetitive transcranial magnetic stimulation to the primary motor cortex interferes with motor learning by observing. *J. Cogn. Neurosci.* 21, 1013–1022
71. McGregor, H.R. *et al.* (2018) Changes in corticospinal excitability associated with motor learning by observing. *Exp. Brain Res.* 236, 2829–2838
72. Bernardi, N.F. *et al.* (2013) Observing motor learning produces somatosensory change. *J. Neurophysiol.* 110, 1804–1810
73. Ostry, D.J. and Gribble, P.L. (2016) Sensory plasticity in human motor learning. *Trends Neurosci.* 39, 114–123
74. McGregor, H.R. and Gribble, P.L. (2017) Functional connectivity between somatosensory and motor brain areas predicts individual differences in motor learning by observing. *J. Neurophysiol.* 118, 1235–1243
75. Simon, H. (1962) The architecture of complexity. *Proc. Am. Philos. Soc.* 106, 467–482
76. Bechtel, W. and Richardson, R.C. (1993) *Discovering Complexity Decomposition and Localization as Strategies in Scientific Research*, Princeton
77. Krakauer, J.W. *et al.* (2017) Neuroscience needs behavior: correcting a reductionist bias. *Neuron* 93, 480–490
78. Cole, M.W. *et al.* (2013) Multi-task connectivity reveals flexible hubs for adaptive task control. *Nat. Neurosci.* 16, 1348
79. Duncan, J. (2010) The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* 14, 172–179
80. Petersen, S.E. and Posner, M.I. (2012) The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* 35, 73–89
81. Torriero, S. *et al.* (2007) The what and how of observational learning. *J. Cogn. Neurosci.* 19, 1656–1663
82. Aquino, T.G. *et al.* (2020) Value-related neuronal responses in the human amygdala during observational learning. *J. Neurosci.* 40, 4761–4772
83. Lambon Ralph, M.A. *et al.* (2017) The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18, 42–55
84. Jefferies, E. (2013) The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex* 49, 611–625
85. Binney, R.J. and Ramsey, R. (2020) Social semantics: the role of conceptual knowledge and cognitive control in a neurobiological model of the social brain. *Neurosci. Biobehav. Rev.* 112, 28–38
86. Amodio, D.M. (2019) Social cognition 2.0: an interactive memory systems account. *Trends Cogn. Sci.* 23, 21–33
87. Redcay, E. and Schilbach, L. (2019) Using second-person neuroscience to elucidate the mechanisms of social interaction. *Nat. Rev. Neurosci.* 20, 495–505
88. Shamay-Tsoory, S.G. and Mendelsohn, A. (2019) Real-life Neuroscience: an ecological approach to brain and behavior research. *Perspect. Psychol. Sci.* 14, 841–859
89. Matusz, P.J. *et al.* (2019) Are we ready for real-world neuroscience? *J. Cogn. Neurosci.* 31, 327–338
90. Pinti, P. *et al.* (2018) A review on the use of wearable functional near-infrared spectroscopy in naturalistic environments. *Jpn. Psychol. Res.* 60, 347–373
91. Pinti, P. *et al.* (2020) The present and future use of functional near-infrared spectroscopy (fNIRS) for cognitive neuroscience. *Ann. N. Y. Acad. Sci.* 1464, 5
92. Henschel, A. *et al.* (2020) Social cognition in the age of human-robot interaction. *Trends Neurosci.* 43, 373–384
93. Apšvalka, D. *et al.* (2019) Fluid intelligence and working memory support dissociable aspects of learning by physical but not observational practice. *Cognition* 190, 170–183
94. Marr, D. (1982) *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*, W.H. Freeman & Company
95. Kaplan, D.M. (2017) Integrating mind and brain science: a field guide. In *Explanation and Integration in Mind and Brain Science* (Kaplan, D.M., ed.), pp. 1–28, Oxford University Press
96. Kriegeskorte, N. and Douglas, P.K. (2018) Cognitive computational neuroscience. *Nat. Neurosci.* 21, 1148–1160
97. Kaplan, D.M. and Hewitson, C.L. (2021) Modelling Bayesian computation in the brain: unification, explanation, and constraints. In *Neural mechanisms: new challenges in the philosophy of neuroscience* (Calzavarini, F. and Viola, M., eds), pp. 11–33, Springer, Springer Nature, Cham, Switzerland. (Studies in Brain and Mind; vol. 17)
98. Niv, Y. (2020) The primacy of behavioral research for understanding the brain. *PsyArXiv* Published online October 22, 2020. <http://dx.doi.org/10.31234/osf.io/y8mxe>
99. Barrett, H.C. (2012) A hierarchical model of the evolution of human brain specializations. *Proc. Natl. Acad. Sci.* 109, 10733–10740
100. Ramsey, R. and Ward, R. (2020) Putting the nonsocial into social neuroscience: a role for domain-general priority maps during social interactions. *Perspect. Psychol. Sci.* 15, 1076–1094
101. Spunt, R.P. and Adolphs, R. (2017) A new look at domain specificity: insights from social neuroscience. *Nat. Rev. Neurosci.* 18, 559–567
102. Michael, J. (2015) A. D’Ausilio, Domain-specific and domain-general processes in social perception – a complementary approach. *Conscious. Cogn.* 36, 434–437
103. Churchland, P.M. (2013) *Matter and Consciousness* (3rd edn), MIT Press
104. Bassett, D.S. *et al.* (2011) Dynamic reconfiguration of human brain networks during learning. *Proc. Natl. Acad. Sci.* 108, 7641–7646
105. Li, Q. *et al.* (2019) Dynamic reconfiguration of the functional brain network after musical training in young adults. *Brain Struct. Funct.* 224, 1781–1795
106. Kao, C.-H. *et al.* (2020) Functional brain network reconfiguration during learning in a dynamic environment. *Nat. Commun.* 11, 1–13
107. Lenartowicz, A. *et al.* (2010) Towards an ontology of cognitive control. *Top. Cogn. Sci.* 2, 678–692
108. Poldrack, R. *et al.* (2011) The cognitive atlas: toward a knowledge foundation for cognitive neuroscience. *Front. Neuroinformatics* 5
109. Kimble, G.A., ed (1961) *Hilgard and Marquis' "Conditioning and Learning"*, Appleton-Century-Crofts
110. Rizzolatti, G. and Sinigaglia, C. (2016) The mirror mechanism: a basic principle of brain function. *Nat. Rev. Neurosci.* 17, 757–765
111. Cross, E.S. *et al.* (2012) Robotic movement preferentially engages the action observation network. *Hum. Brain Mapp.* 33, 2238–2254
112. Arnold, A.J. and Winkelman, P. (2020) The mimicry among us: intra- and inter-personal mechanisms of spontaneous mimicry. *J. Nonverbal Behav.* 44, 195–212
113. Heyes, C. (2011) Automatic imitation. *Psychol. Bull.* 137, 463–483
114. Iacoboni, M. (2009) Imitation, empathy, and mirror neurons. *Annu. Rev. Psychol.* 60, 653–670
115. Gariépy, J.-F. *et al.* (2014) Social learning in humans and other animals. *Front. Neurosci.* 8, 58
116. Busching, R. and Krahé, B. (2020) With a little help from their peers: the impact of classmates on adolescents' development of prosocial behavior. *J. Youth Adolesc.* 1–15
117. Cumming, J. and Eaves, D.L. (2018) The nature, measurement, and development of imagery ability. *Imagin. Cogn. Pers.* 37, 375–393
118. Eaves, D.L. *et al.* (2016) Motor imagery during action observation: a brief review of evidence, theory and future research opportunities. *Front. Neurosci.* 10, 514
119. Vogt, S. *et al.* (2013) Multiple roles of motor imagery during action observation. *Front. Hum. Neurosci.* 7, 807
120. Rizzolatti, G. and Craighero, L. (2004) The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192
121. di Pellegrino, G. *et al.* (1992) Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91, 176–180
122. Rizzolatti, G. *et al.* (1996) Localization of grasp representations in humans by PET. 1. Observation versus execution. *Exp. Brain Res.* 111, 246–252
123. Decety, J. *et al.* (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120, 1763–1777
124. Buccino, G. *et al.* (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404
125. Cattaneo, L. and Rizzolatti, G. (2009) The mirror neuron system. *Arch. Neurol.* 66, 557–560

126. Kilner, J.M. and Lemon, R.N. (2013) What we know currently about mirror neurons. *Curr. Biol. CB* 23, R1057–R1062
127. Mukamel, R. *et al.* (2010) Single-neuron responses in humans during execution and observation of actions. *Curr. Biol.* 20, 750–756
128. Willingham, D.B. (1998) A neuropsychological theory of motor skill learning. *Psychol. Rev.* 105, 558
129. Kirsch, L.P. and Cross, E.S. (2018) The influence of sensorimotor experience on the aesthetic evaluation of dance across the life span. *Prog. Brain Res.* 237, 291–316
130. Heyes, C.M. and Foster, C.L. (2002) Motor learning by observation: evidence from a serial reaction time task. *Q. J. Exp. Psychol. A* 55, 593–607
131. Bird, G. and Heyes, C. (2005) Effector-dependent learning by observation of a finger movement sequence. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 262
132. Bird, G. *et al.* (2005) Sequence learning by action, observation and action observation. *Br. J. Psychol.* 96, 371–388
133. Wu, H.G. and Smith, M.A. (2013) The generalization of visuomotor learning to untrained movements and movement sequences based on movement vector and goal location remapping. *J. Neurosci.* 33, 10772–10789
134. Dunne, S. and O'Doherty, J.P. (2013) Insights from the application of computational neuroimaging to social neuroscience. *Curr. Opin. Neurobiol.* 23, 387–392
135. Charpentier, C.J. *et al.* (2020) A neuro-computational account of arbitration between choice imitation and goal emulation during human observational learning. *Neuron* 106, 687–699.e687
136. Wheatley, T. *et al.* (2019) Beyond the isolated brain: the promise and challenge of interacting minds. *Neuron* 103, 186–188
137. Jolly, E. and Chang, L.J. (2019) The flatland fallacy: moving beyond low-dimensional thinking. *Top. Cogn. Sci.* 11, 433–454