

26 The Impact of Action Expertise on Shared Representations

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Abstract

Expertise in the motor domain is something we recognize almost instantaneously in other people, whether a gymnast performing a double layout with a twist, a basketball player slam dunking the ball, a Super-G skier descending a steep course at 80 mph, or a dancer executing 11 consecutive spins on one leg without stopping. While we might be able to readily recognize expertise in others, the degree to which action experts can coordinate or move their bodies in profoundly different ways to non-experts raises intriguing questions for those interested in shared representations between self and other in our social world. Namely, how does an observer's ability to embody an action impact how she perceives that action, and how might perception change as further experience with the observed action is acquired? In this chapter, we address these questions by considering empirical research that explores the relationship between an actor and an observer's motor abilities, and how expertise impacts this relationship.

Introduction

When Mikhail Baryshnikov, one of the most celebrated ballet dancers of all time, takes the stage to perform the lead role in the ballet *Apollo*, observers are instantly aware that, though they also embody a human form that is ostensibly similar to Baryshnikov's, there is a fundamental difference between the body sitting in the theater seat and the body moving on stage. That difference lies in the way Baryshnikov can coordinate his limbs to execute soaring leaps or a dizzying succession of pirouettes, moves which, if most observers were to attempt them, would bear little resemblance to Baryshnikov's. Expertise in the motor domain is something we recognize almost instantaneously in other people, and entire industries rely on some individuals being able to execute sometimes extreme feats of motor control, such as what might be seen in professional sport or performing arts domains. While we might be able to readily recognize expertise in others, the degree to which action experts can coordinate or move

their bodies in profoundly different ways to non-experts raises intriguing questions for those interested in shared representations between self and other in our social world. Namely, how does an observer's ability to embody an action impact how she perceives that action, and how might perception change as further experience with the observed action is acquired?

In this chapter, we address these questions by considering empirical research that explores the relationship between an actor and an observer's motor abilities, and how expertise impacts this relationship. As many of the chapters in this volume illustrate (see Catmur; Dolk & Prinz; Hamilton; Press, this volume, Chapters 22, 1, 15 and 16, respectively), the idea that perception and action share a common cognitive architecture dates back at least to the time of William James (1890). Over recent years, since the discovery of mirror neurons within the premotor and parietal cortices of rhesus macaques, psychology and cognitive and social neuroscience have witnessed a surge in interest in the mechanisms supporting coupling between action and perception (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). The discovery of mirror neurons in the monkey brain provided critical evidence in support of a direct matching or common coding account of how the primate brain navigates between perception and action (Gallese, Rochat, Cossu, & Sinigaglia, 2009; Hommel, Musseler, Aschersleben, & Prinz, 2001; Prinz, 1990, 1997). Moreover, this discovery has inspired hundreds if not thousands of studies into the existence, properties and functionality of such neurons or neural mechanisms in the human brain (for a critical review, see Gallese, Gernsbacher, Heyes, Hickock, & Iacoboni, 2011).

The present chapter focuses on shaping the relationship between action and perception at behavioral and neural levels by different kinds of sensorimotor experience. Due to the fact that much of our own research on action experience and expertise uses dance as a model system for exploring complex action competency, we focus on studies from this domain. However, work from sports, martial arts, music and other relevant domains also informs our understanding of the relationship between expertise and social perception, and other chapters in this volume provide detailed analysis of expertise in these domains (in this volume, for sporting expertise considerations, see Urgesi & Makris (Chapter 27) and Collins & Hill (Chapter 28); for more on music expertise, see Keller, Novembre, & Loehr (Chapter 14) and Waclawik, Watson, & Grah (Chapter 29)). To build the most comprehensive understanding of how sensorimotor expertise impacts perception, we first examine how the brains and behavior of individuals who are recognized as experts in a specific domain (such as professional dancers) differ from those with no such expertise during task performance. Next, we explore what controlled training paradigms reveal in terms of emergence of action expertise among

expert and novice dancers. After we consider how longstanding and newly acquired sensorimotor expertise impact perception, we consider how individuals lacking motor expertise perceive actions performed by an expert mover. The penultimate section takes a slightly broader view of what kinds of action representation are or are not likely to change based on acquired experience. Finally, we conclude with a framework of how shared representations are shaped by sensorimotor experience, and discuss a number of open questions and possible future directions.

The Impact of Longstanding Expertise on Perception

This section elaborates on how longstanding motor expertise is reflected at behavioral and neural levels. The concept of expertise can be described as in-depth knowledge of a particular field. The domain that concerns this chapter is acquired knowledge in the motor domain. The summary or storage of all motor knowledge an individual has acquired during his lifetime is known as a motor repertoire. A motor repertoire is like a vocabulary of actions where each action representation contains information related to a specific action (how to perform the action, how it feels to perform it, what it looks like, what it means, and so on; see Box 26.1 for more information on action representations). Each person's motor repertoire is unique and defined by the movements he has learnt. At the same time, an individual's motor learning is constrained by two factors. First, learning is constrained by general features and limitations of human anatomy. We are prisoners in our bodies, with fixed degrees of freedom for how we can move, mainly guided by the flexion and extension capacities of the joints (i.e. I only can bend my knee or fingers in one direction). Second, our motor repertoires are defined by our own individual physical experience profiles, which might be quite limited for some people, while others spend thousands of hours training in sport, dance, music, martial arts or other specialized physical activities. Nearly every person naturally acquires the ability to perform common motor patterns, such as walking, running, grasping or gripping. On top of these basic actions, however, we can train to perform far more complex and precise actions. For example, in order to execute the perfect arabesque on stage, the prima ballerina has undergone long hours of training, facilitating the acquisition of a large set of motor commands related to this action (flexibility, timing, balance, rhythm and proprioception), which are stored in a distributed network that composes her motor repertoire.

As with any other kind of experience, motor experience is likely to modulate behavior via modified neural responses. In the following section, we describe how longstanding expertise modulates perception of actions at the neural and behavioral levels.

Box 26.1 Action representations

An *action representation* holds information about a motor act. Depending on the context, this idea has also been termed motor representation, motor repertoire or motor schema. These alternative names may refer to the whole action representation or to just some of its components. Jeannerod's (1997) concept of action representation is similar to Arbib's (1981) motor schema concept. The latter was introduced as a concept to integrate information from perception, action and memory and described how knowledge from these domains was stored and applied. For other authors, such as Schmidt (1975), this schema is the core of complex connections between action's motor and sensory components. Interestingly, Schmidt's schema idea moves away from classical views that consider the motor program as a centralized and predetermined reflex chain, towards a definition that links past action memories and current action effects in a time–experience interaction.

From a cognitive perspective, goal-directed actions are internally guided. They can each be described as a sequence of stages that includes goal identification, intention, planning towards that goal, motor programming and motor execution. Motor representations hold information about processes associated with movements we have learned to execute. Besides these purely motor processes, we store related information that has been associated with particular actions via learning, either during execution or other learning modalities. In this way, motor patterns may be very well linked with information from other modalities, such as vision (e.g. how the action looks), audition (e.g. a clapping action is associated with a particular sound), proprioceptive information (how it feels to perform a specific action), semantic information (action meaning, e.g. a waving movement means 'bye'), intention (e.g. grasping a glass means he wants to drink), and so on. Therefore, action representations are multimodal. When an action representation is activated, an individual has access to action information from all these modalities related to that particular action.

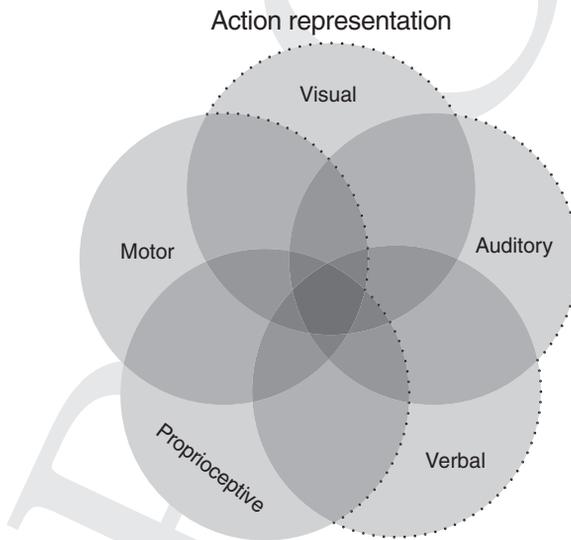
The individual motor repertoire

Each person's motor repertoire is unique, comprising the motor acts she has learnt. While some actions are very common (i.e. grasping, walking) and can likely be found in the motor repertoire of most people, others are more idiosyncratic and can be found only in motor repertoires of those individuals who have learnt them via training (i.e. riding a bike, juggling, performing a pirouette). While action representations are multimodal in general, one may acquire action information from only a selection of modalities. For example, blind individuals' action representations lack visual information about how an action looks, but still retain other related information linked to the motor commands (auditory, proprioceptive, meaning, and so on).

Equally, one can have a good visual representation of how an action looks and its associated sound and meaning without having performed it (lacking the motor component; i.e. an avid diving spectator watching the high dive competition in the Olympics).

Since the discovery of the mirror neuron system, evidence has emerged to suggest that an action representation is activated in an observer when she watches the same action performed by another agent. This suggests a shared mechanism that links the observer (me) with the executor (other). To investigate what sensory components are shared during observation, researchers have compared brain responses in participants who differ in the information stored in their individual motor repertoire (see main text of this chapter; also see Urgesi & Makris, this volume, Chapter 27).

The figure illustrates an action representation schema, including information from different sources. Please note that other action cognitive information such as goals and intentions are not represented in this schema. This diagram aims to represent the possibility of storing multisensory information about any given action. For example, with motor training, information from all the modalities can be stored. The section circumscribed by the red dotted line represents information from an action that has been acquired only through observation, but whose motor programs have never been learnt. Similar segregations can occur excluding other modalities (visual, auditory, verbal/semantic).



Box 26.1 Action representation schema, including information from different sources. *See Plate 19.*

Neuroimaging Evidence

Thanks to the discovery of mirror neurons in the ventral premotor and parietal cortices of the primate brain (Gallese et al., 1996; di Pellegrino et al., 1992; Rizzolatti et al., 1996), we know that overlapping neural codes are recruited whether watching or performing the same action. This discovery provided neural evidence for a *shared* neural system for action observation and execution in the primate brain. Early fMRI action observation studies used paradigms modified from the original electrophysiological work performed with non-human primates involving observation of simple goal-directed actions such as grasping and reaching. These studies consistently reported activation in the ventral premotor cortex, parietal cortex and superior temporal sulcus (a region often associated with perception of social stimuli and biological motion (Allison, Puce, & McCarthy, 2000; Grossman, Battelli, & Pascual-Leone, 2005) during action observation (Decety et al., 1997; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes & Decety, 2001). These early fMRI studies provided a strong foundation for understanding which regions of the human brain are engaged during observation of simple goal-oriented actions. However, this early work could not discriminate between a general sensorimotor response during observation and a specific internal motor simulation of the observed action.

Calvo-Merino and colleagues were interested in exploring the extent to which brain activation during action observation truly reflects resonance between an observed action and one's specific motor repertoire. To do this, they designed a series of studies using longstanding expertise. Their expertise model is based on the *individuality* of one's motor repertoire (based on individual learned movements), and the *similarity* of the motor repertoire of those individuals who received similar training. In a first fMRI study, they chose two groups of participants (dancers) who were trained in different movement vocabularies that were kinematically similar: classical ballet and capoeira (a Brazilian martial art that features dance and acrobatics). Having two expert groups was important to ensure that putative effects were not due to a simple experience effect (i.e. larger repertoire and motor abilities in the expert group than in the control, non-expert group). The researchers compared brain responses of ballet and capoeira dancers, as well as non-expert controls, in an action observation paradigm where all participants watched three-second video-clips of ballet and capoeira movements (Figure 26.1a). Participants were asked to watch the videos and perform a dummy task to ensure they were paying attention to the stimuli. Considering the action–execution matching theory associated with mirror neurons (cf. Rizzolatti & Craighero, 2004), the authors predicted stronger brain responses in mirror system regions when participants observed a movement that has previously been learnt (i.e. it resides within the

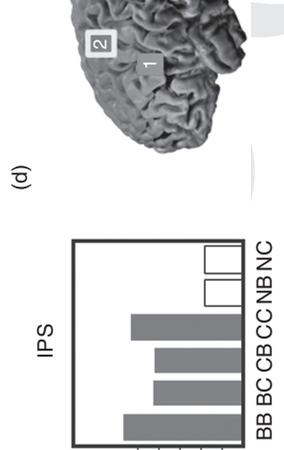
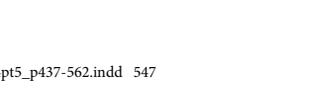
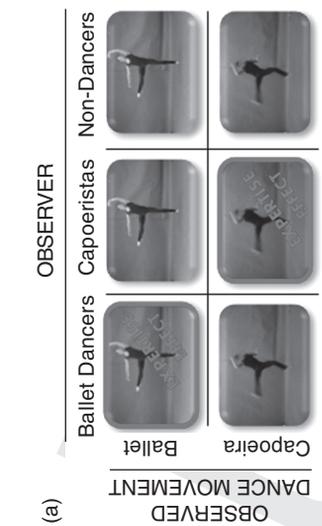


Figure 26.1 Results from Calvo-Merino et al. (2005, 2006) concerning long-standing dance expertise and brain engagement. See *Plate 17*.

Notes: (a) Schema of 2x3 design using expert observers. The expertise effect is determined by interaction group (observer: ballet dancers, capoeiristas, non-dancers) and type of observed movement (ballet movements, capoeira movements).

(b) Parameter estimates for the expertise effect during action observation in left precentral gyrus/dorsal premotor cortex (-24 -6 72), left intraparietal sulcus (-33 -45 54). In both brain regions, parameter estimates show that the effect of expertise is driven by a crossover interaction between the two groups of observer expert dancers and the two types of observed action. Movement

Figure 26.1 (*cont.*)

type has minimal effects in non-dancers. BB: ballet dancers viewing ballet; BC: ballet dancers viewing capoeira; CB: capoeira dancers viewing ballet; CC: capoeira dancers viewing capoeira.

(c) Schema of 2x2x2 design using experts with visual and motor familiarity (green outline) and only visual familiarity (no outline). Yellow outline indicates the effect of seeing a performer of your own gender. This effect is canceled out by subtracting a similar version from common motor acts, where all dancers have equal visual and motor experience.

(d) Schema of standard brain activations significant at (1) ventral premotor, (2) dorsal premotor, (3) SPL, (4) IPS, and (5) pSTS. Red squares show activations sensitive to the expertise effect (modified from Calvo-Merino et al., 2005). Areas in a yellow square are also significantly active for the purely motor expertise effect (modified from Calvo-Merino et al., 2006).

observer's acquired motor repertoire), compared with an unlearned, unfamiliar movement.

The interaction between group (ballet, capoeira and controls) and type of observed movement (ballet, capoeira) revealed a specific effect of expertise (Figure 26.1d). This was manifest as an effect of watching familiar movement (ballet dancers watching ballet, and capoeira dancer watching capoeira) compared to activations while watching unfamiliar movement (ballet dancers watching capoeira, and capoeira dancer watching ballet). Specifically, this interaction showed significant activation in the premotor cortex (ventral and dorsal sections), superior parietal lobe, intraparietal sulcus and posterior superior temporal sulcus (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). This pattern of findings suggests that neural responses during action observation are modulated by the relationship between the observed action and the observer. The control group of non-dancers did not show differentiated responses within the described areas while watching ballet or capoeira moves. Overall, these results suggest that neural engagement of these regions during observation of familiar actions may provide access to a form of shared action representation, at the neural level, between the observer and the performer.

However, an intriguing question was raised by this work. This question concerns *which* component of an action representation is retrieved during observation. More specifically, does action observation predominantly engage purely motoric mechanisms, over and above the visual representation of the action or semantic knowledge of the action (also see Box 26.1)? In order to answer this question, it is necessary to disentangle an observer's experience associated with different components of an action representation. After several interactions with dancers and choreographers, Calvo-Merino and colleagues became aware of an important factor through which classical ballet movements are classified that served their research purposes exceptionally well.

Classical ballet features gender-specific movements (i.e. movements that are trained and performed by only one gender) and gender-common movements (i.e. movements trained and performed by both genders). Therefore, female dancers trained in classical ballet will have acquired motor training of female-specific moves, and vice versa for male dancers. However, as female and male dancers train and perform together, both genders acquire visual familiarity and semantic knowledge about all the movements, regardless of gender specificity. As such, Calvo-Merino and colleagues designed a subsequent experiment that enabled the dissociation of visual and motor familiarity, to test for brain regions that might respond to an internal simulation of the action in specifically *motor* terms, over and above any associated visual or semantic representations (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006).

Similar to the Calvo-Merino et al. (2005) study, the follow-up experiment again used an action observation task. Now female and male classical ballet dancers served as participants and watched three-second video-clips of gender-specific dance movements. These movements were performed by a female dancer and a male dancer, dressed in black clothes (Figure 26.1c). The dancers also watched a set of dance movements commonly performed by both genders, to rule out any possible effects related to observing a female or a male dancer. In order to dissociate purely motor and visual representations during observation of gender movements, it was essential that only classical ballet dancers trained *specifically* in their respective gender movement vocabulary (and not in the opposite gender moves) participated in the study. To ensure that dancers' prior motor training adhered to gender-defined conventions, all dancers completed a preliminary questionnaire enquiring about how often they performed and watched the individual movements used in the experiment in their professional training. The questionnaire showed that male dancers were visually familiar with both male and female movements, but only motorically familiar with the male-specific movements, and the opposite was true for the female dancers. This control was particularly important as it is becoming increasingly common for the 'rules' of classical dance to be broken in order to create novel performances.¹ The neuroimaging results from this study were straightforward and conclusive (see Figure 26.1d). In order to find areas tuned by purely motor resonance with the observed action, rather than other action-related information (such as visual or semantic knowledge), the authors compared brain activity related to gender-specific movement (controlling for visual or semantic knowledge) with classical ballet movements common to both genders in two female and male dancers and a control group. They found that, during observation of motorically familiar movements, brain activity was

¹ For examples, see Les Ballets Trockadero de MonteCarlo, www.trockadero.org, or Matthew Bourne's *Swan Lake*, www.swanlaketour.com, in which male dancers perform typically female ballet vocabulary.

stronger in three brain regions: the premotor cortex in the left hemisphere, and the bilateral superior parietal lobe and cerebellum. Again, because the experimental design controlled for visual familiarity and other information associated with the actions, it was possible to relate the activation in these areas to direct internal motor resonance.

It is of note that brain responses in both studies by Calvo-Merino and colleagues (2005, 2006) shared a common set of areas classically identified as core nodes of the human mirror system (the premotor and parietal cortices). These regions, jointly with the cerebellum (Calvo-Merino et al., 2006), are involved in making motor responses and also coding observed actions. Activations related to general expertise were also found in the STS (Calvo-Merino et al., 2005), but this region did not show significant responses for purely motor experience (Calvo-Merino et al., 2006). This confirms that STS may play an active role during observation of familiar movements, but its response must be related to features of the action such as visual or semantic familiarity rather than strictly motor familiarity. When truly motor resonance is isolated, STS does not appear to participate (ibid). Subsequent work by Orgs, Dombrowski, and Jansen-Osmann (2008), using a similar expertise paradigm in which dancers and non-dancers watched dance sequences and everyday movements, showed reduced desynchronization when expert dancers watched familiar movements compared to non-dancers observing the same stimuli.

Overall, the above studies employing individuals with longstanding expertise suggest specific neural substrates are responsible for a shared representation between observer and performing agent based on the type of action information that both individuals have in common. As psychological scientists, we need to further explore if this differentiated neural response associated with expertise has implications at the behavioral level. This matter is addressed in the following section.

Behavioral Evidence

There are myriad examples of expert observers being able to spot nuances in skilled performers' actions that those of us watching from home could never spot, such as judges of diving, gymnastics or ice skating in the Olympic Games. How is it that expert judges are able to see small details that the couch potato observer cannot? Visual sensitivity enhancement by experience has been demonstrated in other domains using expertise (e.g. car experts, bird experts; Gilaie-Dotan, Harel, Bentin, Kanai, & Rees, 2012; Kirsch et al., 2013; Seligman & Reichenberg, 2009). However, this type of expertise is due simply to high levels of visual exposure. As we have seen in the previous section, expertise in the action domain is multisensory. Is Olympic judges' visual acuity impressive due to the fact that many of them have been practitioners of

the same sport they are judging, or is this simply a matter of extensive visual practice, which implies that any of us could reach that level of perception? (For deeper consideration of this question, also see Urgesi & Makris, this volume, Chapter 27).

A study by Calvo-Merino, Ehrenberg, Leung, and Haggard (2010) sought to address this question. This question was precisely evaluated by comparing dance experts' performance in a simple visual discrimination task of dance movements. Four groups of participants took part in this study; female and male expert dancers, and female and male non-experts. The gender factor was important as participants observed two types of dance movement: female gender-specific and gender-common movements (following the gender specialization existing in classical ballet described in the previous section). Therefore, while no differences were expected between the female and male non-experts, any interaction between gender and the type of movement in the expert dancer group would indicate that motor and visual expertise play separate roles in perception of action. To facilitate a broad spectrum of performance across expertise levels on the behavioral task, the authors created a set of stimuli using point-light displays (PLDs), a technique commonly used to study biological motion, whereby points of lights are attached to the main joints of a performing agent while actions are recorded in a dark room (Johansson, 1973). PLDs were created of several female dancers performing the same dance movements. The task consisted of watching pairs of dance videos depicted as PLDs and judging whether the pairs depicted the same or different videos. Video pairs always depicted the same movements, which were performed by either the same dancer or two different dancers. This was a difficult task, as classical ballet dancers are trained such that their performance minimizes any possible idiosyncrasies that could be used to differentiate between the dancers.

As expected, the control group performed the task significantly worse than experts, and no interaction with gender was found. Interestingly, both the female and male dancers performed the task with a similar accuracy. This result suggests that visual sensitivity to others' actions significantly improves with expertise; however, once it reaches a specific level of expertise (motorically and visually) there appears to be little room for behavioral improvement.

Other studies have addressed the effect of expertise or familiarity in the visual domain from a different perspective. For example, in an interesting set of experiments, Loula, Prasad, Harber, and Shiffrar (2005) compared performance on action recognition and agent identification tasks while participants observed PLDs of unknown people (strangers) and friends. Performance was significantly better during observation of a friend performing idiosyncratic movements (e.g. free dancing) as compared to the other conditions (i.e. a stranger performing actions or a friend or stranger performing common movements). This visual familiarity effect represented in the ability to recognize our friends' actions

highlighted the effect that mere visual exposure may have on action discrimination. To rule out whether purely motor experience makes an additional unique contribution to action perception, Casile and Giese (2006) performed an elegant training study whereby only motor patterns were learnt in the absence of any associated visual response (participants were blindfolded while they underwent motor training). This study demonstrated significantly better visual discrimination of physically trained (without vision) motor actions. To date, these results provide the best evidence to support the additional behavioral role of motor codes during action perception (in addition to any ongoing visual effects).

The Impact of Experimentally-Induced Expertise on Perception

Another way to explore how motor (or visual) experience with complex action shapes perception is to induce expertise in an experimental context. The benefit of probing the impact of experience on perception in the laboratory is that the actual amount of time a person has spent rehearsing or watching an action can be carefully manipulated and measured, which in turn enables researchers to take a closer look at how the specific amount of experience (or actual performance ability) impacts perception. Naturally, this approach is not without its limitations, as the kind of expertise for the actions being studied has not built up over a lifetime of deliberate practice, or at least 10,000 hours spread over 10 years (the time required for achieving skilled professional status in a motor skill; Ericsson, Krampe, & Tesch-Romer, 1993). However, when studies using such approaches are considered in tandem with those examining perception of experts who have considerably more, and varied, practice with a motor skill (such as those described the 'Neuroimaging Evidence' and 'Behavioral Evidence' sections above), a more complete picture of how visuomotor experience shapes perception begins to emerge. This section first considers the neuroimaging evidence of how experience shapes perception before moving on to discuss the limited behavioral work investigating the impact of *de novo* action representations on perception.

Neuroimaging Evidence

While a growing number of studies have investigated the impact of complex action training manipulations on action perception, the body of evidence is still modest. The first study that reported such a manipulation was performed by Cross, Hamilton, and Grafton (2006), and followed a company of expert contemporary dancers as they learned a new 25-minute work of dance across a six-week rehearsal period. The dancers were invited into the laboratory

each weekend across the rehearsal period, where they underwent fMRI whilst watching short video segments of the choreography they were rehearsing as well as kinematically similar movements that they never physically rehearsed. The dancers' task whilst in the scanner was to watch each movement and imagine themselves performing it, and at the end of each video assign a rating based on how well they thought they could reproduce the particular movement segment at present. When the authors compared brain activity across all scanning sessions when the dancers watched rehearsed movement compared to the kinematically similar non-rehearsed movement, they found a pattern of activity comprising parietal, premotor and superior temporal cortices that was very similar to that reported by Calvo-Merino and colleagues (2005) when they compared ballet experts watching ballet compared to capoeira or capoeira experts watching capoeira compared to ballet. The novel discovery by Cross and colleagues emerged when the dancers' ratings of their own performance ability were added to the neuroimaging data as parametric modulators, designed to reveal which brain regions showed increasing levels of activity the better the dancer could perform the observed movement. This analysis revealed activity increases in the two core mirror system regions, namely, the left ventral premotor cortex and inferior parietal lobule (Figure 26.2a). The authors suggest that this finding shows that the more adept an observer becomes at performing an action, the more he simulates that action when observing it.

Shortly after Calvo-Merino and colleagues reported on the impact of visual compared to physical experience on perception among expert ballet dancers (Calvo-Merino et al., 2006), Cross and colleagues conducted a training study to address a complementary question. This question pertained to how visual and physical experience with complex, full-body actions impacts brain and behavior. Cross and colleagues (2009) started with a group of dance-naïve participants and trained them to dance a number of sequences over five days of training using a popular dance video game similar to 'Dance Dance Revolution'. During each day of physical practice, participants spent an equivalent amount of time watching a different (but similar) set of dance sequences that they never physically practiced. A third set of dance sequences remained untrained. In this study, participants underwent fMRI scanning on the very first day of the study (before any training procedures began) and after the fifth and final day of training concluded. During scanning, participants watched and listened to the soundtracks of each of the sequences from the (to-be) physically trained, (to-be) observationally trained and (to-be) untrained sequences. After all scanning and training procedures were completed, participants returned to the laboratory to perform all sequences (from the danced, observed and untrained conditions) with the dance video game, which enabled objective scoring of physical performance across all training categories.

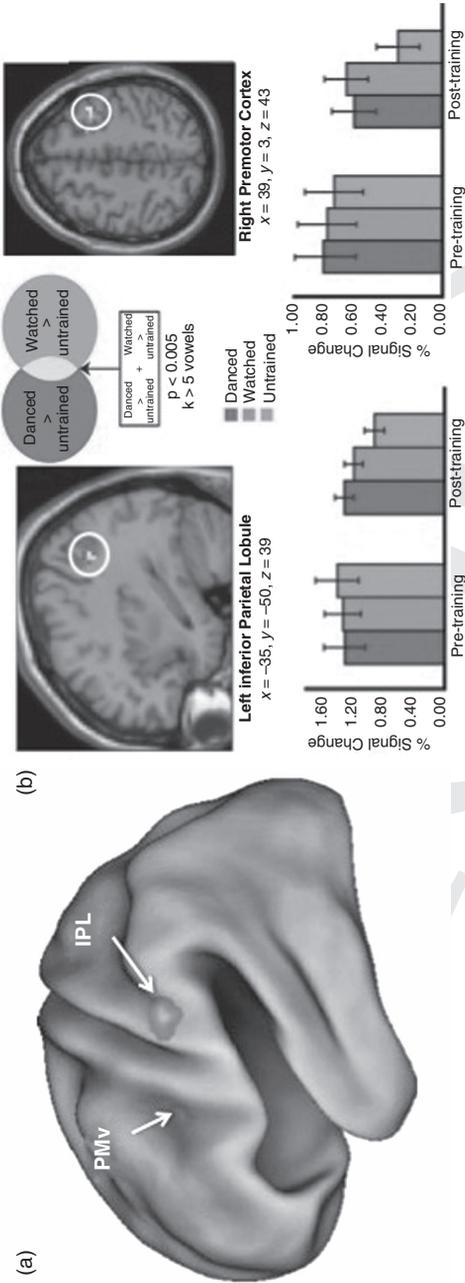


Figure 26.2 Results from Cross et al. (2006) concerning physical expertise and action embodiment. See Plate 18.

Notes: (a) Using parametric analyses that took dancers' ability ratings into account, the authors found that left ventral premotor cortex (PMv) and inferior parietal lobule (IPL) showed an increasingly robust response when dancers watched movements they were most expert at physically performing.

(b) Brain regions emerging from the conjunction analysis evaluating overlap between physically practiced > untrained sequences (red activations/bars) and watched > untrained sequences (blue activations/bars) from the training study performed with novice dancers. The parameter estimate plots beneath the brains illustrate the response within the left inferior parietal lobule (left) and right premotor cortex (right) during the pre-training and post-training scans when participants observed music video-clips from the different training sequences during fMRI.

Sources: (a) Modified from Cross et al. (2006). (b) Modified from Cross et al. (2009).

After the five days of physical and observational training, participants performed the physically practiced sequences the best, the untrained sequences the poorest, and performance for the observed sequences was at an intermediate level between practiced and untrained sequences (ibid). It is of note that participants were never explicitly told to try to learn the sequences they observed during daily training, and were not told until the final day of the study they would be asked to perform these sequences. Participants were simply told to sit and watch a few sequences in between physical training bouts to reduce their heart rate. Thus, the evidence of performance gains from visual experience alone likely represents incidental learning from passive observation. This fact is more striking in light of the imaging findings (Figure 26.2b). In a conjunction analyses performed to reveal brain regions that respond to practiced compared to untrained sequences and observed compared to untrained sequences in a similar way, two sensorimotor brain regions emerged: the left inferior parietal lobule and the right premotor cortex. It is of note that the parameter estimates from this analysis (illustrated by the bar plots below the brain images in Figure 26.2b) show that, after the five days of training, neither of these brain regions discriminated between sequences that were physically practiced or visually experienced (see red and blue bars from the post-training plots). In a noteworthy counterpoint to what Calvo-Merino and colleagues showed with expert male and female ballet dancers, Cross and colleagues showed that, in dance-naïve participants, a week of physical practice with one set of movements and visual experience with another set leads to similar responses within parts of the parietal and premotor cortices. However, in the direct contrast of physical > observational practice, Cross et al. (2009) found greater activity in the right dorsal premotor cortex. While not the extensive network of brain regions found by Calvo-Merino et al. (2006) to be more responsive to physical compared to visual experience (also see Figure 26.1d), some correspondence between the two studies did emerge, and in particular revealed a role for dorsal premotor cortex in specifically *physical* action experience.

Together, these studies demonstrate the utility of combining behavioral training with neuroimaging measures to explore the impact of action expertise on action perception (see Box 26.2 for more detail on training studies). As highlighted in the ‘Neuroimaging Evidence’ section above, the imaging work provides important insights into the neural signature of expertise, but behavioral work is every bit as crucial for developing and exploring these insights. In the following section, a brief overview of some of the laboratory-induced action expertise work is presented that underscores this point.

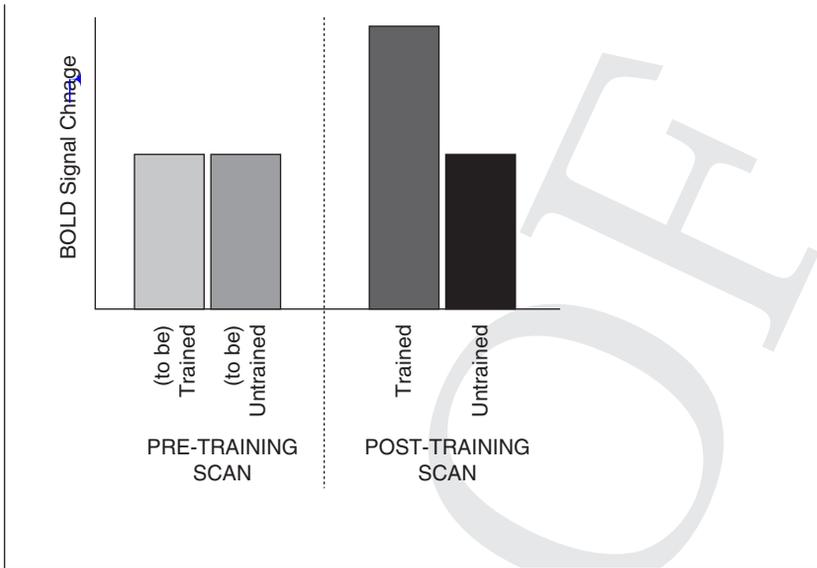
Box 26.2 Training expertise

Training studies help to build a more complete picture of how action expertise shapes perception through rigorous experimental control of participants' exposure to trained versus untrained tasks. Moreover, training studies afford the opportunity to quantify the impact of a training intervention per se, by comparing behavioral performance or brain activity before and after training. The figure illustrates one approach to running training studies where identical fMRI sessions are separated by a period of several days of identical behavioral training sessions. In some studies, particularly those investigating training experience in the non-motor domain (such as visual/observational or auditory experience with actions), participants return to the laboratory to physically perform all actions experienced during training (testing day 7 in the timeline figure; Cross et al., 2009; Kirsch et al., 2013; Kirsch, Dawson, & Cross, 2015). Such training paradigms have also been used to examine the impact of training visual expertise for actions an observer cannot physically execute, such as those performed by expert gymnasts or non-human agents (Cross et al., 2013).

Another benefit of implementing identical pre- and post-training fMRI sessions when examining the impact of laboratory-based training experience is that they enable precise quantification of how behavior has changed due to the training intervention. In other words, by evaluating the interaction of greater brain activity during the post-training scan in the trained > untrained condition, compared to the pre-training scan to be trained > to remain untrained conditions, it is possible to identify where in the brain the BOLD signal change is *specific* to the training intervention, and not due to spurious differences between stimuli or actions that were trained compared to those that remained untrained. The figure illustrates this – if data were collected during a post-training scan only, it would be impossible to rule out the possibility that some differences existed in terms of how the brain responded (or, indeed, how participants physically performed) to stimuli in the red (trained) and blue (untrained) groups. However, the combined use of targeted training interventions with pre- and post-training fMRI measures enables a closer look at (and elimination of) this possibility when done correctly.



Box 26.2 An approach to running training studies where identical fMRI sessions are separated by a period of several days of identical behavioral training sessions. See Plate 20.



Neurophysiology and Behavioral Evidence

Laboratory-based training experiments have helped to illuminate how experience shapes perception in a number of ways. Elegant work linking training experience with mirror neuron activity comes from work with non-human primates. The researchers who originally discovered mirror neurons described how, after long periods of experimentation, they noticed that mirror neurons seemed to generalize their responses to actions performed by non-biological effectors, such as tools (Arbib & Rizzolatti, 1999). Ferrari, Rozzi, and Fogassi (2005) empirically followed up on this anecdote by training monkeys to perform actions with the hand, arm or mouth, and to observe actions performed by a hand, mouth or tool. The authors found that, after two months of training, a certain subset of neurons in premotor area F5 responded most strongly when the monkeys observed actions performed by a tool. The authors conclude that the training experience enabled the monkeys to extend their action understanding capacity to actions for which they lack a strict corresponding motor representation, thus speaking to the flexibility of neural circuitry underlying action understanding (*ibid*).

A rich literature of training studies with human participants has also yielded important insights into how behavioral training shapes perception (for a review of some of this work, see McGregor & Gribble, this volume, Chapter 25). One study discussed above bears particular mention, in terms

of its innovative approach and the importance of its findings. This was the study by Casile and Giese (2006), where participants learned to perform a novel upper-body movement while blindfolded, with only verbal and haptic feedback. After this non-visual learning, the authors asked the participants to visually identify non-visually learned actions. The authors found that not only were participants able to identify the visual test pattern of the non-visually learned movement after training, but also that the accuracy with which participants could execute the performed movement correlated positively with visual recognition performance. As such, this training study provided another critical piece of support for the notion that changes in one's motor repertoire result in changes in perception (ibid).

A more recent line of work has investigated how training manipulations might impact another side of perception, namely, an observer's *affective* response to a perceived action (Kirsch et al., 2013, 2015; Kirsch, Snagg, Heerey, & Cross, 2016). In these studies, participants learned to perform complex dance sequences in a video game context that uses whole-body motion tracking to quantify performance. The authors were interested in assessing how participants' affective responses when watching these dance sequences changed after they had spent time physically practicing them, simply observing them or only listening to the music that accompanies them. Using both between-subjects (Kirsch et al., 2013) and within-subjects (Kirsch et al., 2016) designs, the authors found that participants enjoyed watching dance movements more after they had spent time either physically practicing them or passively observing them. Listening to the soundtrack only had no impact on the enjoyment participants derived from watching the movements. These studies demonstrate that an observer's affective response to watching others in action presents yet another avenue for exploring the impact of laboratory-induced training experience on perception (also see Orgs, Caspersen, & Haggard, this volume, Chapter 30, for a more detailed discussion of the relationship between an actor, an observer and aesthetics).

As highlighted in Box 26.2, laboratory-based behavioral training studies provide a rich opportunity for inducing *de novo* experience in the visual, motor or visuomotor domains to explore how newly acquired experience shapes perceptual or motor behavior. Naturally, a limitation of this approach is that it is often not possible to train the level of expertise in participants that is possible with studies looking at longstanding expertise, such as those discussed earlier in this chapter. However, taken together, both the longstanding expertise and the laboratory-induced training experiments provide complimentary approaches for probing how experience shapes perception.

Summary and Future Directions

When watching others in action, whether Mikhail Baryshnikov performing on stage or a jogger crossing the road, an observer's prior experience with these actions profoundly shapes how he perceives them. Over the past decade, research from both our laboratories has used dance as a model to explore how observers' longstanding or newly acquired motor repertoires influence perception. This work has demonstrated that sensorimotor regions of the brain associated with the human mirror system are more engaged when dancers watch movements they are experienced in performing (Calvo-Merino et al., 2005), and that the better they are at performing an observed action, the more the left inferior parietal and ventral premotor cortices are engaged (Cross et al., 2006). Moreover, work with expert male and female ballet dancers demonstrates that actual physical experience with particular actions engaged these brain regions above and beyond visual experience only (Calvo-Merino et al., 2006). However, a training study with novice dancers learning a fast-paced dance video game demonstrates that a week's worth of visual or visuomotor experience with dance sequences shows similar impact on parts of parietal and premotor cortices (Cross et al., 2009). In the behavioral domain, evidence has been found with expert and novice dancers that the differentiated neural signatures for expert and non-expert actions reported in the neuroimaging studies are further borne out behaviorally, with evidence showing that action expertise increases visual sensitivity to others' actions (Calvo-Merino et al., 2010) as well as impacts an observer's enjoyment when watching an action (Kirsch et al., 2013, 2016).

It is perhaps unsurprising that the research discussed in this chapter raises many more questions than it answers. Two substantial outstanding questions concern whether *all* action representations are malleable based on experience, and the extent to which embodiment (or 'embodiability') of an observed action matters for how it is perceived and understood. Recent work with amputees (Aziz-Zadeh, Sheng, Liew, & Damasio, 2012; Liew, Sheng, & Aziz-Zadeh, 2013a; Liew, Sheng, Margetis, & Aziz-Zadeh, 2013b) and observing actions performed by non-human robots (Cross et al., 2012) or human or artificial agents that move in ways observers cannot (Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2013) suggests that actions likely do not need to be embodied (or even 'embodiable') in order for experience with them to shape sensorimotor cortical engagement or behavior. However, this line of inquiry remains ripe for further exploration and exploitation, as possibilities for shaping or instilling (physical) action representations via visual input alone are of great interest to those working in stroke rehabilitation (Garrison, Aziz-Zadeh, Wong, Liew, & Winstein, 2013), as well as in physical therapy, sporting, dance and martial arts contexts.

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