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Inside the brain of an elite athlete: what processes support high achievement in sports?

Kielan Yarrow, Peter Brown & John W. Krakauer

Preface

Events like the World Championships in athletics and the Olympic games raise the public profile of competitive sports. They may also leave us wondering what sets the competitors in these events apart from those of us who simply watch. Here we attempt to draw links between neural and cognitive processes that have been found to be important for elite performance, and computational and physiological theories inspired by much simpler laboratory tasks. In this way we hope to incite neuroscientists to consider how their basic research might help explain sporting skill at the highest levels of performance.

Introduction

Year on year, competitive athletes confound our expectations regarding the limits of human physical performance. Although expert performance has been studied within cognitive psychology for many years ¹, this research has had limited impact on our understanding of its neural basis because the emphasis is on complex real-world tasks assessed with performance measures that do not map easily onto computational processes or their neural implementation. Conversely, the focus of the neuroscientists has been on much simpler laboratory-based tasks. These tasks are more amenable to bridging the brain-behaviour divide because they allow more rigorous psychophysical characterization, computational modelling and brain-based hypothesis testing with single-unit recording and brain imaging. However, the relationship between simple lab-based motor adaptation tasks (learned over hours and days) and sports skills (learned over months and years) is far from clear.

Consideration of what is required to be good at sport leads to the realization that distinctions between perception, cognition and motor control are fuzzy at best ². If

maintaining the domains of perception, cognition, and action is useful for heuristic purposes then evidence suggests that athletes develop practice-dependent task-specific skills in all three domains.

In this Review, we introduce current computational and neurophysiological models of motor control and skill learning, including optimal feedback control, with its focus on attaining precision and consistency in the high-level action goal. We then focus on some of the properties that distinguish expert sportspeople from beginners, such as predictive rather than reactive decisions to sporting scenarios, and suggest how these abilities may involve both the mirror system and an expanded role for forward models which includes predicting the sporting consequences of actions. We also link our account to neurophysiological data suggesting interdependency between decision making and action planning. Hence we will attempt to identify how learning principles and neurophysiology could account for the observed performance differences with the aim of bridging the gap between psychological research on expertise and neuroscientific models of the basic mechanisms that support sporting success.

Current ideas in motor control

All movements have goals. This is especially true in sport, where the goal is to win. Movements also have energetic costs. Thus the efficient computation or skilled movement is the one that is optimal in terms of accomplishing the goal at the lowest cost. In a recent formulation of the computational motor control framework, optimal feedback control^{3,4}, three basic kinds of computation can be described: first, we need to be able to accurately predict the sensory consequence of our motor commands (*forward model*; see *Box 1*); second, we need to combine these predictions with actual sensory feedback to form a belief about the state of our body and the world (*state estimation*); third, given this state estimate we have to adjust the gains of our sensorimotor feedback loops so that our movements can maximize some measure of performance after optimally balancing the costs and rewards of the movement (*optimal control*).

The areas involved in the above computations remain controversial. The cerebellum may house forward models as cerebellar patients fail to take account of their own actions to anticipate the required change in grip force when catching a dropped

object ⁵, and when transcranial magnetic stimulation (TMS) is used to produce a virtual lesion of the lateral cerebellum, reaching behaviour suggests an out-of-date estimate of initial arm position ⁶. Other areas which have also been linked to the optimal control framework include the parietal cortex, which may be crucial for integrating the output of forward models with sensory feedback to provide estimates about the state of the body, and the premotor and motor cortices that might implement the predictive control policy ⁷, ⁸. Finally, the basal ganglia may either provide a motor motivation signal, which is then used to compute the “cost-to-go”, or be where the “cost-to-go” is computed ⁸.

What does optimal control suggest about the movements of elite athletes? A naïve prediction might be that because experts achieve a more consistent end result, the entire trajectory of their movements should be more consistent from trial to trial. However, the multiple degrees of freedom available to the motor system mean that end-point consistency might still be accompanied by variability in both final postures and earlier components of a movement ⁹. Movement possibilities multiply further when the desired outcome is a consequence of the movement (like a golf ball’s trajectory) rather than a component of the movement (like the terminal position of a reach).

Simple movements do show striking regularities ^{10,11} and movement patterns do seem to stabilise with practice ¹². However, stabilisation is greatest for those aspects of posture that contribute directly to the desired outcome, whereas other parameters are relatively variable ^{9,13,14}. For example, in a quick-draw pistol shooting task, joint angles were determined at different points in the movement ¹⁵. In this study the variance in joint angles, measured from trial to trial, was decomposed into a component that did not affect pistol alignment with the target (because different joints compensated for one another) and a component that did ¹³. Variance was higher for the former component than the latter, suggesting flexibility in specifying the precise movement path so long as the correct outcome was achieved.

Athletes also fail to reproduce a precise kinematic pattern when performing a particular sports-specific activity ¹⁶. This seems sensible, given that sporting scenarios are often erratic, so goal-directed actions will rarely be initiated from an identical starting situation. Indeed there is evidence from experiments using prolonged microstimulation that neurones in primary motor cortex (M1) drive movements towards a consistent end

point regardless of the initial posture¹⁷. What matters is the outcome of the movement, not the movement itself. This idea has been updated computationally in terms of the minimum intervention principle and the unconstrained manifold hypothesis — the central idea is that variance is only reduced along dimensions that are relevant to task accomplishment and is allowed to float in non-relevant task dimensions^{4, 13}. Furthermore, highly stereotyped movements limit the opportunity for learning, which would seem to require that we try out different strategies to determine the mapping of motor commands onto outcomes¹⁸. An interesting example of this has been demonstrated in bird song learning where basal ganglia circuits induce state-dependent variability for purposes of motor exploration during learning¹⁹.

Skill development and motor learning

Basic properties of skill development

What do we mean by sports skill? At what level (perceptual, cognitive or motor) is an athlete's skill manifest? Does an Olympic basketball player just jump higher and throw more accurately than non-athletes or are higher-order perceptual and planning skills also present? And how specific is an athlete's skill? Would the basketball player be better than a non-athlete at another sport like table tennis?

Skill is a level of performance in any given task that can only be acquired through practice. Indeed, skilled professionals of any stripe can be considered people who have had the motivation to practice one thing far more (approximately 10,000 hours in 10+ years²⁰) than most people could endure (see Boxes 2 and 3). Across a wide range of tasks the relationship between one measure of skill, the speed of task completion, and trials spent practicing is well approximated by a power law²¹ (see Figure 1). This implies that performance continues to improve with task-relevant practice indefinitely, although the rate of improvement declines over time. Of course, most of the relevant data comes from tasks learnt for short periods of time in the laboratory. However, it is worth highlighting one classic study reporting performance at an industrial cigar rolling task²². Workers were included who had produced in excess of ten million cigars over seven years of work. They were still getting faster!

Computational principles in motor learning

Currently, the optimal feedback control framework outlined above does not address learning: the optimization is predicated on already optimal forward models, state estimation, and knowledge of execution noise and the relevant cost function. Most computational studies that have investigated motor learning have focussed on error-based learning using adaptation paradigms, for example force fields or visuomotor rotations²³,²⁴. However, the link between adaptation and genuine skill development is questionable. For example, the adaptation of a single-arm reaching movement, which occurs when novel forces are experienced, is retained only partially when the same movement must be made in a bimanual reaching context²⁵. This may have implications for athletic training regimens which assume skill transfer, such as single arm swimming. Moreover, the precise roles of explicit awareness, attention, motivation, and reward for adaptation have not been extensively investigated, but these factors are likely to be much less important for adaptation than they are for the skill learning required for high achievement in sport. This can be understood intuitively by imagining donning prism glasses and being instructed “don’t adapt” – this will not work; as we will adapt away reaching errors whether we want to or not. Indeed, in a recent study of rotation adaptation, the forward model was learned at the expense of the goal of the task²⁶. For learning motor skills, by contrast, explicit awareness of what is required²⁷, attention and motivation may all be essential components. The framework that is most likely to be applicable to skill acquisition is reinforcement learning (RL; e.g.²⁸). The two most important characteristics of RL are trial-and-error search and learning in the face of delayed reward. Three important sub-elements of RL are a policy, a reward function and a value function.

This framework is immediately intuitive when it comes to sports, where learning is guided by successes as well as errors, and also explains why coaches are so useful. A coach can direct the trial-and-error search and thereby reduce the parameter space that needs to be explored to find the ideal policy, and they can prevent an athlete from falling into local maxima for immediate rewards by evaluating a local action with respect to the future goal of winning, and thereby allow the athlete to attain the global maxima with maximal sum of future rewards (value). Indeed RL theory has an actor/critic architecture that directly parallels the player/coach dichotomy²⁹. A recent study supports the

usefulness of coaching by showing that subjects do not necessarily choose the optimal long-term learning strategy when allowed to choose on their own³⁰. More recent reinforcement models include the fourth element of planning through a simulation of the environment (essentially the same as a forward model introduced above). A skilled athlete could be considered a person who has learned very good forward models at various levels of representation, which allows them to plan a better movement in any given context. For example, a professional tennis player has learned an accurate forward model of their arm, their racket, and even of the actions of their opponent (see later). This knowledge allows the player to decide on the best control policy for that moment in time.

Neurocognitive basis of skill development

Although it is clear that improvement through practice applies just as well to cognitive activities (such as chess and language) and occurs over extended periods of time, most research on the neural bases of skill acquisition has concerned low-level perception or motor execution over the short-term. Increased perceptual skill is associated with various changes in primary sensory cortex including map expansion^{31,32}, sharpening of neural tuning³³ and alteration in temporal response characteristics of neurons³⁴. Interestingly, these changes at early cortical stages of information processing appear to be under top-down control. Hence an experienced athlete might more efficiently bring attentional resources to bear on the most important stimulus attributes required for low-level processing. This was demonstrated in action video game players, who were found to have enhanced selective visual attention compared to non-game players³⁵. However, evidence for improved general attentional abilities in athletes is mixed^{36,37}, in apparent contrast with their demonstrably superior sports-specific search skills (see later).

Laboratory studies suggest that increases in speed and accuracy in motor task performance are associated with changes in M1, similar to those seen in the primary visual cortex (V1) for perceptual learning. For example, in rats skill-related increases in cortical map representation have been reported, along with increases in synapses per neuron in layer V of M1³⁸. In monkeys, long-term practice of a specific reaching sequence over years is reflected in activity of specific neurons in M1³⁹, while in humans, TMS and functional imaging have revealed changes in M1 representation associated with

repetition of simple thumb movements⁴⁰ and with skilled sequential finger movements⁴¹.

In cognitive psychology, theoretical descriptions of changes in skilled performance have tended to follow the Fitts pattern: cognitive to associative to autonomous⁴². The key concept is that of increasing automaticity: where controlled processes are attention demanding, conscious and inefficient, automatic processes are rapid, smooth, effortless, demand little attentional capacity and are difficult to consciously disrupt⁴³. There is evidence from dual-task experiments that novice hockey players, footballers and golfers are affected strongly by concurrent tasks (e.g. monitoring a sequence of tones for a target), whereas experts show relative immunity, suggesting highly automatic performance^{44, 45}. Indeed, experts can become undone when they are forced to interrogate the actions they are producing (see Box 4).

Crucially, it is not automaticity *per se* that is indicative of skill but the level of skill at which automaticity is attained. Recent formulations describing the development of expertise suggest that most of us fail to develop beyond a hobbyist level of performance precisely because we settle into automaticity at a level we find enjoyable rather than continuing to interrogate our skills⁴⁶. Hence automaticity represents a false ceiling, not a measure of excellence. Here we instead consider a useful operational definition of motor execution skill to be the ability to defy the speed-accuracy trade-off for a given task. In other words a skilled tennis player can serve faster *and* be more accurate than a novice who serves more slowly. Thus sporting skill at the level of motor execution can be thought of as acquiring a new speed-accuracy trade-off relationship for the sub-tasks that make up a given sport.

One recent study showed that transcranial direct current stimulation (tDCS) centred over contralateral M1 and applied during training on a novel skill enhanced skill acquisition (defined as a change in the speed accuracy trade-off function) over multiple days through an effect on between-day consolidation⁴⁷. Interestingly, tDCS did not affect the rate of learning within day or the retention of motor learning over a three month period after training. This study supports the idea that M1 plays a role in skill acquisition and that multiple dissociable mechanisms are involved over the time course of skill learning. Needless to say the ability to use non-invasive cortical stimulation methods to

enhance the level of skill that can be acquired for a given level of practice might have implications for professional athletics.

Expert and novice brains

A small number of studies have looked for structural and physiological differences between novices and expert athletes. TMS can be used to assess expert-novice differences by mapping-out the hand muscle representation in primary motor cortex⁴⁸. Compared with recreational players and non-players, elite racquet-sport athletes show asymmetries in the motor maps of their playing and non-playing hands, as well as differences in the threshold TMS intensity that is required to elicit motor evoked potentials (MEPs)⁴⁹. Interestingly, the muscles of expert tennis players show increased corticospinal facilitation during tennis imagery but not golf or table tennis imagery⁵⁰. This demonstrates a task-specific, practice-induced, interaction between hierarchies of representation: imagery (a cognitive process that involves multiple areas outside of M1) can lead to potentiation of output from M1 (which is involved directly in execution).

Differences in corpus callosum integrity, assessed in humans using diffusion tractography, correlate with inter-individual differences in skill in a bimanual coordination task⁵¹. This result supports the idea that skilled performance can be reflected in macro-structural change. That inter-individual differences in skill acquisition ability might be partly attributable to genetic differences was suggested by a study showing decreased skill learning capacity in subjects with a BDNF polymorphism⁵². This result builds on previous studies testing both monozygotic and dizygotic twins on balance, manual tracking and constrained reaching tasks, which have suggested heritability in both performance levels and rates of improvement⁵³⁻⁵⁵. However, the relative importance of genetics in skill development remains controversial (see Box 3).

Structural and functional imaging studies have also looked at patterns of change *within individuals* across periods of training on motor tasks. Differences found here are unambiguously the product of training (whereas expert–novice differences might instead reflect innate predispositions), but these studies assessed only a limited period of development relative to the acquisition of genuine expertise. Learning to juggle has been associated with increases in grey matter in a number of areas, with the motion-sensitive

middle temporal area (V5) increasing bilaterally in two studies by the same group^{56, 57}. Such structural growth might reflect an increase in cell size, or the growth of new neurones or glial cells, or perhaps an increase in spine density⁵⁸, but appears to reverse when practice ends, even though performance levels remain elevated⁵⁷. This pattern (practice-related change that reverses with cessation of practice) has also been found in primary motor cortex when TMS is used to measure changes in both the cortical mapping and activation threshold of task-relevant muscles⁵⁹.

Functional brain imaging reveals a network of areas associated with the acquisition of visuomotor skills. Various tasks have been used in the scanner, such as learning of motor sequences, adaptation to force fields, and bimanual coordination. In general, a reduction in activity in so called “scaffolding” areas (presumably related to controlled processing early in the Fitts progression), including prefrontal cortex, anterior cingulate cortex, and posterior parietal cortex, is often found to precede changes in activity within sensorimotor regions associated with task performance, such as primary motor cortex and the cerebellum⁶⁰. Differences between expert and novice athletes have also been investigated, but the movement requirements of many sports generate serious challenges. Imaging studies have investigated sports-related processing by asking subjects to reproduce their pre-shot (planning) routines in the scanner. Expert golfers, for example, show increased activation in superior parietal cortex, lateral dorsal premotor cortex, and occipital lobes during this period compared to novices, but novices’ brains show more overall activity, particularly in the basal ganglia and limbic areas⁶¹. This may reflect an inability to filter out inappropriate information. Electroencephalographic (EEG) studies have also suggested that experts may exhibit “neural efficiency”, a tendency towards more discrete neural activations. Differences in alpha power are often observed between novice and expert sportspeople (e.g.⁶²) and may even predict their best performance. For example, sensorimotor event-related desynchronisation in the alpha band is reduced immediately prior to accurate golf strokes by expert golfers when compared to their inaccurate strokes⁶³. Clearly expert and novices use their brains differently, but precisely interpreting these differences in terms of their functional roles seems some way off at present.

Sports-specific decision making

Motor decision-making behaviour

Motor decision making operates at a number of levels. Any given behaviour needs to integrate decisions across a hierarchy of neural representations and types of control signal. All decisions reflect trade-offs between cost and rewards, and it is possible that similar reinforcement principles operate on multiple reward prediction errors coded in variables that are appropriate to their level in the decision hierarchy. The decision processes underlying action selection, and their attendant theories, which have been reviewed recently^{64, 65} are beyond our scope here. Suffice to say that areas in medial frontal cortex and the basal ganglia seem to evaluate both reward and effort costs associated with actions and can choose between conflicting potential actions in a given context. These areas then supervise the areas that have primary control of movement. Skilled athletes are likely to have trained their decision circuits, in a manner analogous to what has been seen in M1, to make quicker and better choices.

People are able to implicitly estimate the magnitude of their own variable error and use it to modify their movements in the light of the experiment's reward context^{66, 67}. In one experiment, subjects jabbed at targets on a screen. Regions of the screen could yield rewards or punishments of various magnitudes, and the precise layout of these regions could be used to predict an optimal target location (in terms of maximising payouts). For some layouts, the optimal location to choose depended on the predicted scatter of a subject's responses. Subjects took account of their own performance to aim at just the right place. The situation is rather like a golfer targeting his shot away from the hole and towards one side of the green in order to avoid the risk of landing in a bunker.

Decision making is typically modelled as a process of information accumulation towards one or more thresholds, which would then trigger specification of the appropriate action⁶⁸⁻⁷⁰. However, one recent neural-network model, building on single-cell data in primates that showed simultaneous activity for different potential reaching directions⁷¹, posits that decision making and motor preparation proceed in parallel (see Figure 2)². Motor plans, represented by distributions of neural activity across a population of cells⁷², are generated for the most relevant actions afforded by the current environment. These

plans compete through mutual inhibitory connections to generate a winner, and this competition represents the decision process, with biasing signals from regions like the pre-frontal cortex tipping the competition in favour of the selected motor act. There is some evidence for the proposed regional interactions in the form of increases in spike-field coherence between frontal and parietal reach areas when decisions are being made freely rather than being constrained⁷³. The model also explains various behavioural effects, such as the way reaching movements are sometimes initially directed towards the centre of two targets⁷⁴; this occurs because population responses overlap. Findings obtained in the saccadic motor system suggest that similar principles may operate there too, albeit with different neural loci^{75,76}.

This parallel interacting model is attractive from the perspective of sports expertise. Going to the trouble of representing many possible actions seems computationally intensive and neurally wasteful, but this solution offers a speed advantage because the brain need not wait to make a decision based on full information before it begins to prepare an action. Instead, it can specify actions in parallel and then pick one based on the best information available. Conversely, a default action can be released early, based on a weighting across action plans if there is no time to wait for full specification⁷⁴. Hence for the elite athlete, continuously modifying the strength of competing action plans based on the probabilistic structure of the current sporting environment seems sensible. In the lab, neurophysiological data suggest that motor areas do specify movements in a way which reflects the moment-by-moment probability in favour of a particular action. Studies using noisy random-dot motion discrimination, in which monkeys produce saccades to indicate their percept, provide a clear example⁶⁵. Stimulating the frontal eye fields at different moments after stimulus onset triggers a saccade that deviates increasingly towards the most likely response, seemingly reflecting the evolution of an analogue decision variable⁷⁷. Hence, motor programming and choice seem to evolve in parallel. Furthermore, spike rates in the lateral intraparietal area rise like a decision accumulator for a particular saccadic response^{78,79}, and microstimulating this area biases responses in a way that is consistent with a shift in the accumulated decision variable⁸⁰. Accumulating activity in frontal eye field motor neurones also predicts motor decisions, as shown recently using a visual search task⁸¹.

Anticipatory information pick-up in expert performers.

Many sports are played under extreme time pressure. A key distinguishing feature of expert performance is the ability to react to sports-specific events with seeming time to spare. This ability often manifests itself in scenarios requiring complex choices, like selecting the right pass in a team sport. In essence, the expert is able to anticipate how a sporting scenario will unfold based on a detailed understanding of situational probabilities. One idea is that an estimate, for example of where a tennis ball will bounce after it has been hit by an opponent, will be optimal if probabilistic expectations (or “priors”) are combined with available sensory evidence. That the brain uses such a Bayesian strategy was recently demonstrated with a paradigm that allowed manipulation of the statistical distribution of the experimental task as well as the level of uncertainty in the sensory feedback ⁸².

Two related methodologies have been key in determining which properties of an unfolding sporting scenario are used by experts to anticipate requirements: temporal and spatial occlusion (see Figure 3). In temporal occlusion, the first part of a scenario is presented, but the action is paused, cutting off information at different points relative to the sportsperson’s response. Groups differing in expertise are required to predict what is going to happen based on this partial information. Spatial occlusion complements this temporal analysis. Sections of the scenario are again presented, but this time particular regions of a visual scene are obscured. Researchers then infer from where the expert derives their advantage.

Research on batting in cricket provides a concrete example. Cricket batsmen must select a shot based on the trajectory of a ball which may travel at up to 160 km per hour. The ball can deviate through the air, and take an additional deviation when it bounces off the pitch before reaching the batsman. Advanced cricketers use information from prior to the moment at which the bowler releases the ball to help determine its trajectory ^{83, 84}. Specifically, they make use of the motion of the bowling arm, in relation to the bowling hand, primarily between the time of front foot impact and ball release ⁸⁵. Differences in information pickup are found between novices and skilled cricketers, but also between

skilled and elite players⁸⁵. The use of advance information has mostly been assessed using first-person still and video stimuli, but is also found in real batting practice using occluding liquid crystal glasses⁸⁶. Finally, eye-movements recorded when batsmen face a bowling machine demonstrate the continued use of information after ball release⁸⁷. A saccade is made to the predicted bouncing point, with subsequent smooth pursuit. Players with greater skill make better use of early flight information to generate the saccade in anticipation of the bounce.

The ability to anticipate the effect of the opponent's body-part kinematics on ball trajectory has now been described for many sports⁸⁸⁻⁹². How is the relevant information used by experts to facilitate their performance? Anticipatory information pickup has been linked to highly developed domain-specific memory structures. To interpret and respond to an unfolding scenario an athlete must first classify it into a recognisable unit. This can be achieved by developing a large bank of suitable instances in a long-term memory store with rapid and flexible access. The original evidence for this view comes from an activity rather less dynamic than high-speed sports: chess. Expert chess players can rapidly recognise patterns of chess pieces, but only if those patterns are consistent with real games^{93,94}. This domain-specific expert advantage is also found for recall and recognition of structured game situations in a wide variety of sports⁹⁵. While recent research has suggested an advantage for expert sportspeople over novices on some nonspecific sensory tasks such as random dot motion discrimination, performance on sports-specific search, memory and anticipation tests are generally far better predictors of sporting accomplishment than performance on more general low-level tests of perception such as visual acuity^{37,96}. The idea that acquired domain-specific memory structures support sophisticated anticipatory decision-making capabilities is certainly plausible, although the causal link remains to be demonstrated.

Somewhat surprisingly, these isolatable components of expert skill have not received much neuroimaging attention. Might part of the expert advantage in interpreting sports-specific scenarios arise from their enhanced ability to generate the very actions they are required to anticipate? One recent study of basketball players found that expert players could judge the outcome of a basketball shot better than professional spectators or novices based only on the kinematics of the throwing action prior to ball release⁹² (See

Figure 2). Furthermore, corticospinal excitability (measured by using TMS over M1 to elicit MEPs in hand muscles) showed a specific pattern of modulation in the elite basketball players that correlated with their use of kinematic information from finger movements to predict ball trajectories: there was increased M1 excitability only for those hand muscles pertinent to ball throwing before the ball left the hand of the player in the video clip.

There are a number of important conclusions to be drawn from this study. First, the idea of an adaptive forward model, which can anticipate the sensory consequences of motor commands seems to have a direct analogy here in the ability to predict ball trajectory from body-segment kinematics. Admittedly, there is a difference in that in this observation case both limb and ball trajectory are coded in sensory coordinates. However, the finding of increased activation in motor areas with action observation suggests that some form of motor command, which mirrors the observed action, can be sent to a forward model. This idea finds support in earlier behavioural work, showing for example that people predict subsequent trajectories best from temporally occluded videos of dart throws when the videos are of their own movements⁹⁷, i.e. when they already have sets of motor commands that parallel the observed action sequence. The existence of the mirror system, which implies an automatic action-simulation capability that is activated without the need to actually perform the action, has been established in numerous studies⁹⁸⁻¹⁰⁰. For the mirror system to be useful in prediction, it would be necessary to show activation related to the kinematics of the observed task and not just to the more abstract representation of the action goal. This has been shown recently: observation of a grasping movement made by another person, in the absence of any motor response by the observer, elicits activation in motor related areas that depends on the laterality and observed viewpoint of the observed hand¹⁰¹. The mirror system may also play an important role in observational learning, which occurs frequently in sports coaching settings¹⁰².

The second important conclusion from the basketball study is that skill has interdependent perceptual and motor components — only the elite athletes showed anticipation and excitability changes before ball take-off. This finding is consistent with imaging work carried out with expert ballet and capoeira dancers: mirror system

activation increased when experts viewed actions from their own repertoire compared to similar actions with which they were not familiar, and subsequent work using gender-specific ballet moves showed that this heightened activation was dependent upon motor, not visual expertise^{103, 104}.

Third, the model put forward by Cisek², along with single unit evidence, of parallel interactive behaviour is compatible with temporal occlusion experiments: elite athletes can extract important stimulus information earlier than novices and thus, begin movement specification earlier. It could be predicted that biasing of the right action occurs earlier and that action selection is superior in elite athletes. Overall, these results show that elite athletes have skills that amount to considerably more than superior execution at the level of strength and the speed-accuracy trade-off.

Conclusions and future directions

As we have seen, elite athletes show not only increased precision in execution but also superior performance at the level of perception, anticipation and decision-making. This superior performance is task-specific and is dependent on extensive practice and, to some degree, innate inter-individual differences. Existing computational models for motor control and reinforcement learning provide a useful framework to formulate both what needs to be learned and how it is acquired in order to attain maximal sporting skills. Single-unit recording and stimulation in animals and functional imaging and non-invasive cortical stimulation in humans reveal evidence for structural and physiological changes in primary sensory and motor cortex with training. It is likely that analogous changes in medial and lateral frontal cortex, posterior parietal cortex and subcortical structures accompany the higher-order perceptual, planning and decision-making skills seen in elite athletes. Ultimately, an understanding of the neural mechanisms that distinguish elite sportspeople from others not only provides a rational basis for refining future training strategies, but may also open up the possibility of predictive physiological profiling and, in time, genotyping, to foretell the likelihood of success at the highest level.

Glossary

Actor/critic architecture – a reinforcement learning architecture where the policy structure (actor) is separate from the value function (the critic).

BDNF polymorphism – variant allelic form of the brain-derived neurotrophic factor gene.

Corticospinal facilitation – increased excitability of the corticospinal tract, measured using motor evoked potentials.

Cost-to-go – the total cost remaining in the current trial, computed by combining expected rewards, end-point variability, effort and related variables.

Decision variable – a single quantity, reflecting the combination of prior beliefs, current evidence and subjective costs and benefits, which is compared with a decision rule to produce a choice.

Degrees of freedom – the number of parameters needed to specify the posture of a mechanical linkage such as the arm.

Execution noise – random fluctuations in motor output that are not present in the central motor command.

Kinematic pattern – a description of the spatial position of body parts over time.

Mirror system – A network of premotor and parietal cortical areas activated by both execution and observation of action.

Neural tuning – a function describing how a neuron modulates its firing rate as the variable it is encoding changes; more precise tuning reflects modulation over a smaller range.

Policy – the mapping between a state and the action to be taken when in that state.

Prism glasses – lenses which distort the visual input received by the eyes, typically displacing it by a set amount.

Random-dot motion discrimination – a task in which observers view a set of short-lived dots moving in random directions and attempt to determine the direction of a subset of dots that move coherently.

Reward function – the mapping between a given state and its associated reward.

Rotation adaptation – an experimental procedure in which artificial visual feedback is presented during reaching movements, indicating a hand position that is rotated by a constant amount relative to the true direction of hand movement.

Spike-field coherence – a measure of frequency-specific shared variance between spiking activity and local field potentials, the latter providing a measure of synaptic potentials in a neural population.

Transcranial direct current stimulation - a technique in which a weak constant current is applied to the brain, modulating neural activity without eliciting action potentials directly.

Transcranial magnetic stimulation – a technique in which a rapidly changing magnetic field is used to induce transient and localised electrical activity in underlying areas of cortex.

Value function – the total amount of reward summed over current and all future states.

Variable error – the scatter in a set of responses around the mean response.

$\text{VO}_{2\text{max}}$ – a measure of aerobic capacity: The maximum volume of oxygen that can be utilized in one minute of exhaustive exercise.

Box 1: Forward Models

A key idea in computational motor control is that the brain is able to predict the imminent change in either a body part's or an object's state that will result from an outgoing command through an internal simulation called a 'forward model' ¹⁰⁵. There is good experimental evidence that forward models enable precise actions that are too fast to rely on the delays that are inherent in sensory feedback ¹⁰⁶⁻¹⁰⁸, allow more precise state estimation ¹⁰⁹, and can be updated through learning ^{26, 107}. For example, when you move your hand from one place to another, the brain can estimate its new position before sensory feedback arrives. An optimal estimate of your hand's position can be obtained by integrating the forward model's prediction with actual visual and proprioceptive feedback. Forward models can also be trained — when discrepancies arise between feedback and a forward model's prediction, for example when wearing prism glasses, then the forward model can adapt to reduce the prediction error.

Is there a useful connection to be made between the idea of a forward model, which predicts the sensory consequences of one's own actions, and prediction of the actions of others in sports, be they an opponent or team mate? We would first need to show that the forward model concept is applicable to external objects in the outside world. A recent study in cats showed that neuronal discharge in the lateral cerebellum was predictive of target motion ¹¹⁰; the authors speculated that such activity could be used in a predictive capacity for target interception. This result might plausibly be extrapolated to an athlete predicting the effect of an opponent's motion on ball trajectory. A final question is how the idea of forward models of the actions of others might relate to the mirror system, which responds to the actions of others. One possibility is that the mirror system sends a command to the cerebellum, which then sends its prediction back to the premotor cortex for subsequent motor planning ¹¹¹.

Box 2: Motivation

Motivation can be considered the mapping between outcomes and their utilities¹¹². This rather formal definition comes from the reinforcement framework and is probably applicable across the hierarchy of decision making in sport. Motivation can be either implicit, based on unconscious calculation of the reward-cost trade-off of a given movement¹¹³, or explicit in response to externally provided rewards. The existence of a hierarchy of rewards, some implicit and others explicit, raises the possibility of conflicts, which might be best resolved through the presence of a coach.

Motivation may improve motor performance through two effects: a general arousing or energising effect, and a more goal-specific component¹¹². An example of the latter is the observation that monkeys make faster and less variable saccades to those targets associated with the most reward¹¹⁴. Recent developments in reinforcement learning suggest that task-specific rewards may operate through increased dopamine-dependent weighting of 'teaching signals' (phasic dopaminergic signals thought to represent the reward prediction error: the difference between the expected and actual reward in a given trial or time step). These are computed from feedback related to the success of a given course of action. This view has received experimental support in the context of explicit choices between actions¹¹⁵, but only recently has it been shown to be relevant to the trial-to-trial learning of a single action, such as a tennis return¹¹⁶.

Although motivation may improve performance and learning tied to rewards in the short-term, the big question in sport is the nature of the motivation underlying the thousands of hours of practice required to achieve elite status. There is evidence to suggest that those who practice the most like it the least²⁰, which might reflect their awareness of the real goal of practice: to get better at what you are doing rather than enjoy it through the experience of short-term rewards. Thus the best athletes may be the ones who are most goal-directed in terms of the "total sum of future rewards" with future rewards receiving the highest weighting.

Box 3: Nature versus nurture in skill acquisition.

The nature–nurture controversy has a long and polarised history^{117, 118}. One position considers all skilled performance, including the elite, to be a monotonic function of the quantity of prior deliberate practice (DP)^{20, 46, 119}. DP is distinct from work (performance at maximal levels) and play (inherently enjoyable skill-related activities). It depends upon concentration, optimised training strategies and feedback. The ability to engage in DP is constrained by resources, the requirement for recuperation and motivation.

Investigations reconstructing the practice histories of high achievers support the DP framework. Internationally competitive athletes engage in DP from an early age, and differ from national and regional competitors in accumulated hours of practice¹²⁰⁻¹²³. Training certainly influences sports-relevant physiological attributes dramatically¹²⁴⁻¹²⁷. However, retrospective practice histories have questionable validity, and autobiographical data yield differing interpretations^{128, 129}. Furthermore, studying high achievers ignores individuals who may have practiced to little avail, and cannot establish the causal direction of the practice-attainment relationship¹³⁰.

Even within groups showing similar attainment, retrospective studies show individual differences in accumulated practice¹²¹. These differences might reflect either degrees of conformity to optimal training, or gene-mediated differences in responses to training. Evidence suggests training-related improvements on $\text{VO}_{2\text{max}}$ and strength have a genetic component^{131, 132}, but heritability coefficient estimates depend on the environmental range under study¹³³, challenging generalisation to elite groups⁴⁶. Furthermore, careful monitoring of conformity to training is necessary to preclude motivational explanations⁴⁶.

What about genetic polymorphisms with known physiological actions? Many genes are of potential relevance¹³⁴⁻¹³⁶. For example the celebrated Finnish skiing triple-Olympic champion, Eero Mäntyranta, possesses a favourably mutated erythropoietin receptor gene that increases his haemoglobin concentration and promotes oxygen supply to brain and muscle¹³⁷. In general, however, more research is needed to clarify how genes and environment affect sporting success^{138, 139}.

Box 4: When sporting skills go wrong

“Choking” under pressure may be defined as unexpectedly impaired performance during competition^{140, 141}. One possible explanation for choking relates to the Fitts pattern in skill development⁴². Highly practiced skills become automatic, so performance may actually be damaged by introspection, which is characteristic of an earlier, consciously-mediated stage¹⁴². Experimental interventions that focus attention on movements rather than external events seem to damage performance, but only for accomplished participants¹⁴³. Anatomically, the left dorsal pre-frontal cortex and right anterior cingulate cortex are activated when subjects re-attend to their movements following motor sequence training¹⁴⁴. The ability to maintain an appropriate focus might also reflect activity in the rostral pre-frontal cortex, which has been implicated in shifting between stimulus-independent and stimulus-oriented modes of thought¹⁴⁵.

Intensive training is also associated with more debilitating conditions, including the overtraining syndrome (or burnout)¹⁴⁶. In some individuals repeated performance is also associated with paradoxical derangement of intensively practiced movement, which may over time pervert other movements of the limb. Sustained sensory input related to the practiced movements is thought to lead to abnormal plastic change in the basal ganglia and sensorimotor cortical areas¹⁴⁷. Amongst sportspeople, such focal dystonia is best known as the “yips” in golfers, but may also affect elite runners, tennis-players and even petanque players¹⁴⁸. Once affected, individuals are usually forced to abandon professional sport.

Figure 1 | The learning curve for skill acquisition

Example learning curves from single subjects practicing over extended periods. The red data come from a choice reaction time task with 1,023 alternatives (comprising all possible patterns available to ten fingers). Each cycle includes one repetition of each alternative, completed over two sessions taking 20-30 minutes each. The blue data come from a duration discrimination task in which different durations (demarcated by two tones) were categorised as either short or long. Q_{50} is a threshold measure, similar to the just noticeable difference, but normalised across sets of stimuli with different mean durations. Each session consisted of 300 trials and took around 40 minutes. Also shown are least-squares fits to a function in the form $y = (A)(x+E)^B + C$, where A, B, C and E are free parameters. A and B are scaling variables, while C reflects asymptotic performance and E is included to reflect prior learning¹⁴⁹. Similar functions have dealt well with data sets in which response time is used to assess performance²¹, but the precise form of the learning function remains controversial¹⁵⁰, as indeed does the idea that a single function (which may imply a single process) accounts for the entire learning curve¹⁵¹. Adapted from¹⁴⁹ and¹⁵².

Figure 2 | Neural substrates of the affordance competition model

Possible neural substrates for a model of parallel motor preparation and decision making based on biased competitive interactions². The model is depicted against the backdrop of a primate brain. Red arrows indicate how information arriving at visual cortex is transformed into motor plans for a range of potential actions. Three example neural populations are represented as square segments in coronal slices. In each case, the spatial distribution of neural activity is shown, with lighter regions corresponding to activity peaks. As actions are specified across the fronto-parietal cortex, representations for individual potential actions compete for further processing. Inputs from areas such as the basal ganglia and prefrontal cortical regions bias this competition (blue arrows). Biasing occurs at multiple interconnected anatomical loci, so the complete network encompasses large portions of the brain. When the representation of one action wins the competition, execution is triggered. The resulting movement generates both external environmental feedback (dashed red arrow) and an internal prediction about feedback via a cerebellar loop (see also Box 1). Reproduced from¹⁵³.

Figure 3 | Anticipatory information pickup by expert athletes.

A. Schematic of temporal occlusion methods alongside representative data showing how highly-skilled, intermediate, and student (“low skilled”) batsmen use kinematic information prior to ball release to anticipate cricket deliveries. Subjects viewed projected movies of an onrushing bowler. The movie was stopped at the point of bowler back foot impact (BFI, green), front foot impact (FFI, blue), ball release (R, red) or after the full delivery (NO, yellow). The graph shows subjects’ ability to discriminate whether the ball swings either away from or into the body of a right-handed batsman for deliveries from a medium-pace bowler. Judgements of ball length and spin deliveries were also investigated, but are not shown here. Highly skilled players performed better than intermediates and novices, and showed a reliable improvement when provided with information from front foot impact to release, taking their predictions above chance. B. Example stills from complementary spatial occlusion experiments in which different parts of the bowler’s body were occluded in a display which terminated at ball release. Here the bowler’s arm has been removed. Both the bowler’s arm and their hand were necessary for experts to anticipate ball direction, suggesting that wrist angle was a critical cue. C. Role of the mirror system in predicting the outcome of a basketball shot. Temporal occlusion showed that expert players utilised advanced information better than expert observers or novices to predict shot success (data not shown). Critically, expert players displayed differential cortical excitability when observing accurate compared with inaccurate shots, with this modulation being specific to the finger muscles at a time when only finger posture predicted shot success. MEP = motor evoked potential. ADM = abductor digiti minimi. Adapted from ⁸⁵ and ⁹².

References

1. Ericsson, K.A. *The road to excellence: The acquisition of expert performance in the arts and sciences, sports, and games* (Erlbaum, Mahwah, NJ, 1996).
2. Cisek, P. Integrated neural processes for defining potential actions and deciding between them: a computational model. *J. Neurosci.* 26, 9761-9770 (2006).

This paper presents a computational model based on biased inhibitory interactions, which combines motor decisions and motor planning in a single parallel process.

3. Todorov, E. Optimality principles in sensorimotor control. *Nat. Neurosci.* 7, 907-915 (2004).
4. Todorov, E. & Jordan, M.I. Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* 5, 1226-1235 (2002).
5. Nowak, D.A., Timmann, D., & Hermsdorfer, J. Dexterity in cerebellar agenesis. *Neuropsychologia* 45, 696-703 (2007).
6. Miall, R.C., Christensen, L.O., Cain, O., & Stanley, J. Disruption of state estimation in the human lateral cerebellum. *PLoS. Biol.* 5, e316 (2007).
7. Scott, S.H. Optimal feedback control and the neural basis of volitional motor control. *Nat. Rev. Neurosci.* 5, 532-546 (2004).
8. Shadmehr, R. & Krakauer, J.W. A computational neuroanatomy for motor control. *Exp. Brain Res.* 185, 359-381 (2008).

An up-to-date review outlining the computational framework of optimal feedback control and using it to interpret neuropsychological deficits and guide thinking about functional localisation in the brain.

9. Bernstein, N. *The coordination and regulation of movements* (Pergamon, New York, 1967).
10. Morasso, P. Spatial control of arm movements. *Exp. Brain Res.* 42, 223-227 (1981).
11. Collewijn, H., Erkelens, C.J., & Steinman, R.M. Binocular co-ordination of human horizontal saccadic eye movements. *J. Physiol* 404, 157-182 (1988).

12. Yang, J.F. & Scholz, J.P. Learning a throwing task is associated with differential changes in the use of motor abundance. *Exp. Brain Res.* 163, 137-158 (2005).
13. Scholz, J.P. & Schoner, G. The uncontrolled manifold concept: identifying control variables for a functional task. *Exp. Brain Res.* 126, 289-306 (1999).
14. Muller, H. & Sternad, D. Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J. Exp. Psychol. Hum. Percept. Perform.* 30, 212-233 (2004).
15. Scholz, J.P., Schoner, G., & Latash, M.L. Identifying the control structure of multijoint coordination during pistol shooting. *Exp. Brain Res.* 135, 382-404 (2000).
16. Bartlett, R., Wheat, J., & Robins, M. Is movement variability important for sports biomechanists? *Sports Biomech.* 6, 224-243 (2007).
17. Graziano, M.S., Taylor, C.S., & Moore, T. Complex movements evoked by microstimulation of precentral cortex. *Neuron* 34, 841-851 (2002).
18. Schmidt, R.A. A schema theory of discrete motor skill learning. *Psychol. Rev.* 82, 225-260 (1975).
19. Kao, M.H., Wright, B.D., & Doupe, A.J. Neurons in a forebrain nucleus required for vocal plasticity rapidly switch between precise firing and variable bursting depending on social context. *J. Neurosci.* 28, 13232-13247 (2008).
20. Ericsson, K.A., Krampe, R.T., & Tesch-Romer, C. The role of deliberate practice in the acquisition of expert performance. *Psychol. Rev.* 100, 363-406 (1993).

This paper introduced the deliberate practice framework, providing an important counterpoint to genetic accounts of elite performance.

21. Newell, K.M. & Rosenbloom, P.S. Mechanisms of skill acquisition and the law of practice in *Cognitive skills and their acquisition* (ed. Anderson, J.R.) 1-55 (Erlbaum, Hillsdale, NJ, 1981).
22. Crossman, E.R.F.W. A theory of the acquisition of speed-skill. *Ergonomics* 2, 153-166 (1959).
23. Shadmehr, R. & Mussa-Ivaldi, F.A. Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* 14, 3208-3224 (1994).
24. Krakauer, J.W., Pine, Z.M., Ghilardi, M.F., & Ghez, C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J. Neurosci.* 20, 8916-8924 (2000).

25. Nozaki,D., Kurtzer,I., & Scott,S.H. Limited transfer of learning between unimanual and bimanual skills within the same limb. *Nat. Neurosci.* 9, 1364-1366 (2006).
26. Mazzoni,P. & Krakauer,J.W. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J. Neurosci.* 26, 3642-3645 (2006).
27. Ghilardi,M.F., Moisello,C., Silvestri,G., Ghez,C., & Krakauer,J.W. Learning of a sequential motor skill comprises explicit and implicit components that consolidate differently. *J. Neurophysiol.*(2008).
28. Law,C.T. & Gold,J.I. Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nat. Neurosci.* 12, 655-663 (2009).
29. Takahashi,Y., Schoenbaum,G., & Niv,Y. Silencing the critics: understanding the effects of cocaine sensitization on dorsolateral and ventral striatum in the context of an actor/critic model. *Front Neurosci.* 2, 86-99 (2008).
30. Huang,V.S., Shadmehr,R., & Diedrichsen,J. Active learning: learning a motor skill without a coach. *J. Neurophysiol.* 100, 879-887 (2008).
31. Recanzone,G.H., Merzenich,M.M., Jenkins,W.M., Grajski,K.A., & Dinse,H.R. Topographic reorganization of the hand representation in cortical area 3b owl monkeys trained in a frequency-discrimination task. *J. Neurophysiol.* 67, 1031-1056 (1992).
32. Recanzone,G.H., Schreiner,C.E., & Merzenich,M.M. Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *J. Neurosci.* 13, 87-103 (1993).
33. Schoups,A., Vogels,R., Qian,N., & Orban,G. Practising orientation identification improves orientation coding in V1 neurons. *Nature* 412, 549-553 (2001).
34. Wehr,M. & Laurent,G. Odour encoding by temporal sequences of firing in oscillating neural assemblies. *Nature* 384, 162-166 (1996).
35. Green,C.S. & Bavelier,D. Action video game modifies visual selective attention. *Nature* 423, 534-537 (2003).
36. Buckles,K.M., Yund,E.W., & Efron,R. Visual detectability gradients: effect of high-speed visual experience. *Brain Cogn* 17, 52-63 (1991).
37. Overney,L.S., Blanke,O., & Herzog,M.H. Enhanced temporal but not attentional processing in expert tennis players. *PLoS. ONE.* 3, e2380 (2008).

38. Kleim, J.A. *et al.* Motor learning-dependent synaptogenesis is localized to functionally reorganized motor cortex. *Neurobiol. Learn. Mem.* 77, 63-77 (2002).
39. Matsuzaka, Y., Picard, N., & Strick, P.L. Skill representation in the primary motor cortex after long-term practice. *J. Neurophysiol.* 97, 1819-1832 (2007).
40. Classen, J., Liepert, J., Wise, S.P., Hallett, M., & Cohen, L.G. Rapid plasticity of human cortical movement representation induced by practice. *J. Neurophysiol.* 79, 1117-1123 (1998).
41. Karni, A. *et al.* Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377, 155-158 (1995).
42. Fitts, P.M. Perceptual-motor skill learning in *Categories of human learning* (ed. Melton, A.W.) 243-285 (Academic Press, New York, 1964).
43. Shiffrin, R.M. & Schneider, W. Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychol. Rev.* 84, 127-190 (1977).
44. Leavitt, J.L. Cognitive demands of skating and stickhandling in ice hockey. *Can. J. Appl. Sport Sci.* 4, 46-55 (1979).
45. Beilock, S.L., Carr, T.H., MacMahon, C., & Starkes, J.L. When paying attention becomes counterproductive: impact of divided versus skill-focused attention on novice and experienced performance of sensorimotor skills. *J. Exp. Psychol. Appl.* 8, 6-16 (2002).
46. Ericsson, K.A. Deliberate practice and the modifiability of body and mind: toward a science of the structure and acquisition of expert and elite performance. *Int. J. Sport Psychol.* 38, 4-34 (2007).
47. Reis, J. *et al.* Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proc. Natl. Acad. Sci. U. S. A.* 106, 1590-1595 (2009).

This paper describes a positive effect of transcranial direct current stimulation on motor learning and thus, suggests a way that skill acquisition could be augmented.

48. Nielsen, J.B. & Cohen, L.G. The Olympic brain. Does corticospinal plasticity play a role in acquisition of skills required for high-performance sports? *J. Physiol* 586, 65-70 (2008).
49. Pearce, A.J., Thickbroom, G.W., Byrnes, M.L., & Mastaglia, F.L. Functional reorganisation of the corticomotor projection to the hand in skilled racquet players. *Exp. Brain Res.* 130, 238-243 (2000).

50. Fourkas,A.D., Bonavolonta,V., Avenanti,A., & Aglioti,S.M. Kinesthetic imagery and tool-specific modulation of corticospinal representations in expert tennis players. *Cereb. Cortex* 18, 2382-2390 (2008).
51. Johansen-Berg,H., la-Maggiore,V., Behrens,T.E., Smith,S.M., & Paus,T. Integrity of white matter in the corpus callosum correlates with bimanual co-ordination skills. *Neuroimage* 36 Suppl 2, T16-T21 (2007).
52. Reis,J. *et al.* Role of brain derived neurotrophic factor (BDNF) in acquisition and long-term retention of a novel visuomotor skill. Society for Neuroscience abstracts: 38th annual meeting . 2008.
Ref Type: Conference Proceeding
53. Williams,L.R. & Gross,J.B. Heritability of motor skill. *Acta Genet. Med. Gemellol. (Roma.)* 29, 127-136 (1980).
54. Fox,P.W., Hershberger,S.L., & Bouchard,T.J., Jr. Genetic and environmental contributions to the acquisition of a motor skill. *Nature* 384, 356-358 (1996).
55. Missitzi,J., Geladas,N., & Klissouras,V. Heritability in neuromuscular coordination: implications for motor control strategies. *Med. Sci. Sports Exerc.* 36, 233-240 (2004).
56. Draganski,B. *et al.* Neuroplasticity: changes in grey matter induced by training. *Nature* 427, 311-312 (2004).

This important paper demonstrated alteration in the human brain's macroscopic structure upon skill learning.

57. Driemeyer,J., Boyke,J., Gaser,C., Buchel,C., & May,A. Changes in gray matter induced by learning--revisited. *PLoS. ONE.* 3, e2669 (2008).
58. May,A. *et al.* Structural brain alterations following 5 days of intervention: dynamic aspects of neuroplasticity. *Cereb. Cortex* 17, 205-210 (2007).
59. Pascual-Leone,A., Tarazona,F., & Catala,M.D. Applications of transcranial magnetic stimulation in studies on motor learning. *Electroencephalogr. Clin. Neurophysiol. Suppl.* 51, 157-161 (1999).
60. Kelly,A.M. & Garavan,H. Human functional neuroimaging of brain changes associated with practice. *Cereb. Cortex* 15, 1089-1102 (2005).
61. Milton,J., Solodkin,A., Hlustik,P., & Small,S.L. The mind of expert motor performance is cool and focused. *Neuroimage* 35, 804-813 (2007).

62. Baumeister, J., Reinecke, K., Liesen, H., & Weiss, M. Cortical activity of skilled performance in a complex sports related motor task. *Eur. J. Appl. Physiol.* 104, 625-631 (2008).
63. Babiloni, C. *et al.* Golf putt outcomes are predicted by sensorimotor cerebral EEG rhythms. *J. Physiol.* 586, 131-139 (2008).
64. Rushworth, M.F. Intention, choice, and the medial frontal cortex. *Ann. N. Y. Acad. Sci.* 1124, 181-207 (2008).
65. Gold, J.I. & Shadlen, M.N. The neural basis of decision making. *Annu. Rev. Neurosci.* 30, 535-574 (2007).
66. Trommershauser, J., Maloney, L.T., & Landy, M.S. Decision making, movement planning and statistical decision theory. *Trends Cogn. Sci.* 12, 291-297 (2008).
67. Trommershauser, J., Gepshtein, S., Maloney, L.T., Landy, M.S., & Banks, M.S. Optimal compensation for changes in task-relevant movement variability. *J. Neurosci.* 25, 7169-7178 (2005).
68. Brown, S.D. & Heathcote, A. The simplest complete model of choice response time: linear ballistic accumulation. *Cognit. Psychol.* 57, 153-178 (2008).
69. Pashler, H. Dual-task interference in simple tasks: data and theory. *Psychol. Bull.* 116, 220-244 (1994).
70. Rosenbaum, D.A. Human movement initiation: specification of arm, direction, and extent. *J. Exp. Psychol. Gen.* 109, 444-474 (1980).
71. Cisek, P. & Kalaska, J.F. Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45, 801-814 (2005).
72. Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B., & Massey, J.T. Mental rotation of the neuronal population vector. *Science* 243, 234-236 (1989).
73. Pesaran, B., Nelson, M.J., & Andersen, R.A. Free choice activates a decision circuit between frontal and parietal cortex. *Nature* 453, 406-409 (2008).
74. Ghez, C. *et al.* Discrete and continuous planning of hand movements and isometric force trajectories. *Exp. Brain Res.* 115, 217-233 (1997).
75. Findlay, J.M. Global visual processing for saccadic eye movements. *Vision Res.* 22, 1033-1045 (1982).

76. McPeck,R.M. & Keller,E.L. Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *J. Neurophysiol.* 87, 1805-1815 (2002).
77. Gold,J.I. & Shadlen,M.N. Representation of a perceptual decision in developing oculomotor commands. *Nature* 404, 390-394 (2000).
78. Shadlen,M.N. & Newsome,W.T. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J. Neurophysiol.* 86, 1916-1936 (2001).
79. Churchland,A.K., Kiani,R., & Shadlen,M.N. Decision-making with multiple alternatives. *Nat. Neurosci.* 11, 693-702 (2008).
80. Hanks,T.D., Ditterich,J., & Shadlen,M.N. Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. *Nat. Neurosci.* 9, 682-689 (2006).
81. Murthy,A., Ray,S., Shorter,S.M., Schall,J.D., & Thompson,K.G. Neural Control of Visual Search by Frontal Eye Field: Effects of Unexpected Target Displacement on Visual Selection and Saccade Preparation. *J. Neurophysiol.*(2009).
82. Kording,K.P. & Wolpert,D.M. Bayesian integration in sensorimotor learning. *Nature* 427, 244-247 (2004).
83. Abernethy,B. & Russell,D.G. Advance cue utilisation by skilled cricket batsmen. *Australian Journal of Science and Medicine in Sport* 16, 2-10 (1984).
84. Gibson A.P. & Adams R.D. Batting stroke timing with a bowler and a bowling machine: A case study. *The Australian Journal of Science and Medicine in Sport* 21, 3-6 (1989).
85. Muller,S., Abernethy,B., & Farrow,D. How do world-class cricket batsmen anticipate a bowler's intention? *Q. J. Exp. Psychol. (Colchester)* 59, 2162-2186 (2006).

A thorough example of how temporal and spatial occlusion techniques can be combined to understand the nature of the expert advantage in anticipation-based decision making.

86. Muller,S. & Abernethy,B. Batting with occluded vision: an in situ examination of the information pick-up and interceptive skills of high- and low-skilled cricket batsmen. *J. Sci. Med. Sport* 9, 446-458 (2006).
87. Land,M.F. & McLeod,P. From eye movements to actions: how batsmen hit the ball. *Nat. Neurosci.* 3, 1340-1345 (2000).

88. Goulet, C. *et al.* [Analysis of advance visual indices in receiving a tennis serve]. *Can. J. Sport Sci.* 13, 79-87 (1988).
89. Abernethy, B. Anticipation in squash: differences in advance cue utilization between expert and novice players. *J. Sports Sci.* 8, 17-34 (1990).
90. Starkes, J.L., Edwards, P., Dissanayake, P., & Dunn, T. A new technology and field test of advance cue usage in volleyball. *Res. Q. Exerc. Sport* 66, 162-167 (1995).
91. Savelsbergh, G.J., Williams, A.M., Van der, K.J., & Ward, P. Visual search, anticipation and expertise in soccer goalkeepers. *J. Sports Sci.* 20, 279-287 (2002).
92. Aglioti, S.M., Cesari, P., Romani, M., & Urgesi, C. Action anticipation and motor resonance in elite basketball players. *Nat. Neurosci.* (2008).

This paper links the mirror system, presumed to play a key role in action understanding, with the anticipatory decision making abilities shown by athletes in response to the movements of their opponents.

93. De Groot, A. *Thought and choice in chess* (Mouton, The Hague, 1978).
94. Chase, W.G. & Simon, H.A. The mind's eye in chess in *Visual information processing* (ed. Chase, W.G.) 215-282 (Academic Press, New York, 1973).
95. Hodges, N.J., Starkes, J.L., & MacMahon, C. Expert performance in sport in *Cambridge Handbook of Expertise* (eds. Charness, N., Ericsson, K.A., Hoffman, R.R. & Feltovich, P.) 471-488 (Cambridge University Press, New York, 2006).
96. Ward, P. & Williams, A.M. Perceptual and cognitive skill development: The multidimensional nature of expert performance. *Journal of Sport and Exercise Psychology* 25, 93-111 (2003).
97. Knoblich, G. & Flach, R. Predicting the effects of actions: interactions of perception and action. *Psychol. Sci.* 12, 467-472 (2001).
98. Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73, 2608-2611 (1995).
99. Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91, 176-180 (1992).
100. Fabbri-Destro, M. & Rizzolatti, G. Mirror neurons and mirror systems in monkeys and humans. *Physiology (Bethesda.)* 23, 171-179 (2008).

101. Shmuelof, L. & Zohary, E. Mirror-image representation of action in the anterior parietal cortex. *Nat. Neurosci.* 11, 1267-1269 (2008).
102. Hodges, N.J., Williams, A.M., Hayes, S.J., & Breslin, G. What is modelled during observational learning? *J. Sports Sci.* 25, 531-545 (2007).
103. Calvo-Merino, B., Grezes, J., Glaser, D.E., Passingham, R.E., & Haggard, P. Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr. Biol.* 16, 1905-1910 (2006).
104. Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., & Haggard, P. Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb. Cortex* 15, 1243-1249 (2005).
105. Wolpert, D.M. & Miall, R.C. Forward Models for Physiological Motor Control. *Neural Netw.* 9, 1265-1279 (1996).
106. Flanagan, J.R. & Wing, A.M. The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J. Neurosci.* 17, 1519-1528 (1997).
107. Wagner, M.J. & Smith, M.A. Shared internal models for feedforward and feedback control. *J. Neurosci.* 28, 10663-10673 (2008).
108. Chen-Harris, H., Joiner, W.M., Ethier, V., Zee, D.S., & Shadmehr, R. Adaptive control of saccades via internal feedback. *J. Neurosci.* 28, 2804-2813 (2008).
109. Vaziri, S., Diedrichsen, J., & Shadmehr, R. Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *J. Neurosci.* 26, 4188-4197 (2006).
110. Cerminara, N.L., Apps, R., & Marple-Horvat, D.E. An internal model of a moving visual target in the lateral cerebellum. *J. Physiol.* 587, 429-442 (2009).
111. Miall, R.C. Connecting mirror neurons and forward models. *Neuroreport* 14, 2135-2137 (2003).
112. Niv, Y. Cost, benefit, tonic, phasic: what do response rates tell us about dopamine and motivation? *Ann. N. Y. Acad. Sci.* 1104, 357-376 (2007).
113. Mazzoni, P., Hristova, A., & Krakauer, J.W. Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *J. Neurosci.* 27, 7105-7116 (2007).

114. Takikawa, Y., Kawagoe, R., Itoh, H., Nakahara, H., & Hikosaka, O. Modulation of saccadic eye movements by predicted reward outcome. *Exp. Brain Res.* 142, 284-291 (2002).
115. Satoh, T., Nakai, S., Sato, T., & Kimura, M. Correlated coding of motivation and outcome of decision by dopamine neurons. *J. Neurosci.* 23, 9913-9923 (2003).
116. Kühn, A.A. *et al.* Motivation modulates motor-related feedback activity in the human basal ganglia. *Curr. Biol.* 18, R648-R650 (2008).
117. Galton, F. *Inquiries into human faculty and its development* (Macmillan, London, 1883).
118. Watson, J.B. *Behaviorism* (Norton, New York, 1934).
119. Howe, M.J., Davidson, J.W., & Sloboda, J.A. Innate talents: reality or myth? *Behav. Brain Sci.* 21, 399-407 (1998).
120. Bloom, B.S. Generalizations about talent development in *Developing talent in young people* (ed. Bloom, B.S.) 507-549 (Ballantine Books, New York, 1985).
121. Starkes, J.L., Deakin, J.M., Allard, F., Hodges, N.J., & Hayes, A. Deliberate practice in sports: what is it anyway? in *The road to excellence: The acquisition of expert performance in the arts and sciences, sports and games* (ed. Ericsson, K.A.) 81-106 (Lawrence Erlbaum, Mahwah, New Jersey, 1996).
122. Helson, W.F., Starkes, J.L., & Hodges, N.J. Team sports and the theory of deliberate practice. *Journal of Sport and Exercise Psychology* 20, 12-34 (1998).
123. Ward, P., Hodges, N.J., Williams, A.M., & Starkes, J.L. Deliberate practice and expert performance: Defining the path to excellence in *Skill acquisition in sport: research, theory and practice* (eds. Williams, A.M. & Hodges, N.J.) 231-258 (Routledge, London, 2004).
124. Jokl, E. The human hand. *International Journal of Sport Psychology* 12, 140-148 (1981).
125. Greksa, L.P. Effect of altitude on the stature, chest depth and forced vital capacity of low-to-high altitude migrant children of European ancestry. *Hum. Biol.* 60, 23-32 (1988).
126. Pelliccia, A. *et al.* Remodeling of left ventricular hypertrophy in elite athletes after long-term deconditioning. *Circulation* 105, 944-949 (2002).

127. Iemitsu,M., Maeda,S., Miyauchi,T., Matsuda,M., & Tanaka,H. Gene expression profiling of exercise-induced cardiac hypertrophy in rats. *Acta Physiol Scand.* 185, 259-270 (2005).
128. Howe,M.J. The childhoods and early lives of geniuses: combining psychological and biographical evidence in *The road to excellence: The acquisition of expert performance in the arts and sciences, sports and games* (ed. Ericsson,K.A.) 255-270 (Erlbaum, Mahwah, New Jersey, 1996).
129. Winner,E. The rage to master: The decisive role of talent in the visual arts in *The road to excellence: The acquisition of expert performance in the arts and sciences, sports and games* (ed. Ericsson,K.A.) 271-302 (Erlbaum, Mahwah, New Jersey, 1996).
130. Sternberg,R.J. Costs of expertise in *The road to excellence: The acquisition of expert performance in the arts and sciences, sports and games* (ed. Ericsson,K.A.) 347-354 (Erlbaum, Mahwah, New Jersey, 1996).
131. Bouchard,C. *et al.* Familial aggregation of VO₂max response to exercise training: results from the HERITAGE Family Study. *J. Appl. Physiol* 87, 1003-1008 (1999).
132. Thomis,M.A. *et al.* Strength training: importance of genetic factors. *Med. Sci. Sports Exerc.* 30, 724-731 (1998).
133. Plomin,R., DeFries J.C., MccClearn,G.E., & McGuffin,P. *Behavioural genetics*(Freeman, New York, 2001).
134. Macarthur,D.G. & North,K.N. Genes and human elite athletic performance. *Hum. Genet.* 116, 331-339 (2005).
135. Wolfarth,B. *et al.* The human gene map for performance and health-related fitness phenotypes: the 2004 update. *Med. Sci. Sports Exerc.* 37, 881-903 (2005).
136. Gonzalez-Freire,M. *et al.* Unique among unique. Is it genetically determined? *Br. J. Sports Med.*(2008).
137. de la Chapelle A., Traskelin,A.L., & Juvonen,E. Truncated erythropoietin receptor causes dominantly inherited benign human erythrocytosis. *Proc. Natl. Acad. Sci. U. S. A* 90, 4495-4499 (1993).
138. Le Galliard,J.F., Clobert,J., & Ferriere,R. Physical performance and Darwinian fitness in lizards. *Nature* 432, 502-505 (2004).
139. Davids,K. & Baker,J. Genes, environment and sport performance: why the nature-nurture dualism is no longer relevant. *Sports Med.* 37, 961-980 (2007).

140. Jordet,G. Why do English players fail in soccer penalty shootouts? A study of team status, self-regulation, and choking under pressure. *J. Sports Sci.* 1-10 (2008).
141. Jordet,G. & Hartmen,E. Avoidance motivation and choking under pressure in soccer penalty shootouts. *J. Sport Exerc. Psychol.* 30, 450-457 (2008).
142. Baumeister,R.F. Choking under pressure: self-consciousness and paradoxical effects of incentives on skillful performance. *J. Pers. Soc. Psychol.* 46, 610-620 (1984).
143. Beilock,S.L., Bertenthal,B.I., McCoy,A.M., & Carr,T.H. Haste does not always make waste: expertise, direction of attention, and speed versus accuracy in performing sensorimotor skills. *Psychon. Bull. Rev.* 11, 373-379 (2004).
144. Jueptner,M. *et al.* Anatomy of motor learning. I. Frontal cortex and attention to action. *J. Neurophysiol.* 77, 1313-1324 (1997).
145. Burgess,P.W., Dumontheil,I., & Gilbert,S.J. The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends Cogn. Sci.* 11, 290-298 (2007).
146. Meeusen,R. *et al.* Prevention, diagnosis and treatment of the overtraining syndrome. *Eur. J. Sports Sci.* 6, 1-14 (2006).
147. Defazio,G., Berardelli,A., & Hallett,M. Do primary adult-onset focal dystonias share aetiological factors? *Brain* 130, 1183-1193 (2007).
148. Adler,C.H., Crews,D., Hentz,J.G., Smith,A.M., & Caviness,J.N. Abnormal co-contraction in yips-affected but not unaffected golfers: evidence for focal dystonia. *Neurology* 64, 1813-1814 (2005).
149. Seibel,R. Discrimination reaction time for 1,023-alternative task. *J. Exp. Psychol.* 66, 215-226 (1963).
150. Heathcote,A., Brown,S., & Mewhort,D.J. The power law repealed: the case for an exponential law of practice. *Psychon. Bull. Rev.* 7, 185-207 (2000).
151. di-Japha,E., Karni,A., Parnes,A., Loewenschuss,I., & Vakil,E. A shift in task routines during the learning of a motor skill: group-averaged data may mask critical phases in the individuals' acquisition of skilled performance. *J. Exp. Psychol. Learn. Mem. Cogn.* 34, 1544-1551 (2008).
152. Kristofferson,A.B. A quantal step function in duration discrimination. *Percept. Psychophys.* 27, 300-306 (1980).

153. Cisek, P. Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 362, 1585-1599 (2007).