Inside the brain of an elite athlete: the neural processes that support high achievement in sports

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Abstract | 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 link neural and cognitive processes that have been found to be important for elite performance with computational and physiological theories inspired by much simpler laboratory tasks. In this way we hope to inspire neuroscientists to consider how their basic research might help to explain sporting skill at the highest levels of performance.

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

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Year on year, competitive athletes confound our expectations regarding the limits of human physical performance. Although expert performance has been studied in cognitive psychology for many years[1], this research has had limited impact on our understanding of the neural basis of expert performance 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, neuroscientists have focused 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 laboratory-based motor adaptation tasks (learnt over hours or days) and sports skills (learnt over months or 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 separate domains of perception, cognition and action is useful for heuristic purposes, then evidence suggests that athletes develop practise-dependent task-specific skills in all three domains.

In this Review, we introduce current computational and neurophysiological models of motor control and skill learning. We then focus on some of the properties that distinguish expert sportspeople from beginners, such as the ability to make predictive rather than reactive decisions to sporting scenarios, and suggest how these properties 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 which suggest that decision making and action planning are interdependent. Hence, we 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, in which the goal is to win. Movements also have energetic costs. Thus, the most efficient computation or the most 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, called 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; BOX 1); second, we need to combine these predictions with actual sensory feedback to form a judgement 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 question of which brain areas are involved in the above computations remains controversial.

Policy
Defines the relationship between a state and the action to be taken.

Cost to go
The total cost remaining in the current trial. It is computed by combining expected rewards, end point variability, effort and other variables.

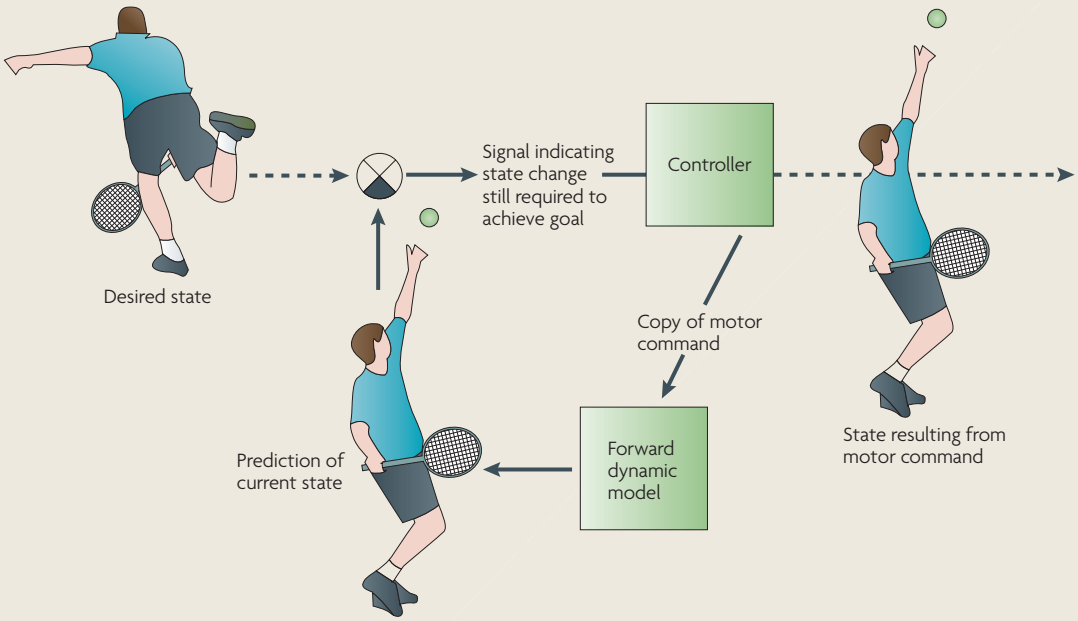
Degrees of freedom
The number of parameters needed to specify the posture of a mechanical linkage such as an arm.

The cerebellum may house forward models, for example patients with cerebellar damage or dysfunction fail to take account of their own actions to anticipate the change in grip force that is required when catching a dropped object[5]. In addition, when transcranial magnetic stimulation (TMS) is used to produce a virtual lesion of the lateral cerebellum, the subject's reaching behaviour suggests that they now have an out-of-date estimate of their initial arm position[6]. Other areas that 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, which 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 naive 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 posture and earlier components of a movement[9]. Movement possibilities multiply further when the desired outcome is a consequence of the movement (for example, a golf ball's trajectory) rather than a component of the movement (for example, the terminal position of a reach).

Simple movements do have striking regularities[10,11], and movement patterns do seem to stabilize with practise[12]. However, stabilization is greatest for those aspects of posture that contribute directly to the desired outcome; 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

Box 1 | **Forward models**



A key idea in computational motor control is that the brain, through an internal stimulation known as a 'forward model', is able to predict the imminent change in the state of either a body part or an object that will result from an outgoing command (see the figure)[105]. There is good experimental evidence that forward models enable precise actions that are too fast to rely on the inherent delays of 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 sensory feedback and a forward model's prediction, for example when wearing prism glasses, then the forward model can adapt to reduce the prediction error.

Can a useful connection be made between a forward model, which predicts the sensory consequences of one's own actions, and a model that could predict the actions of others in sports, be they opponents or team mates? A recent study in cats showed that neuronal discharge in the lateral cerebellum predicts the motion of a moving external target[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. Finally, how does the idea of forward models that predict the actions of others 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].

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 for the latter, suggesting that there was 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 neurons in the primary motor cortex (M1) drive movements towards a consistent end point regardless of the initial posture[17]. 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 reduced only along dimensions that are relevant to task accomplishment and is allowed to increase in non-relevant task dimensions[4,13]. Furthermore, highly stereotyped movements would limit the opportunity for learning, as it seems that we need to try out different strategies to map motor commands onto outcomes[18]. An interesting example of this is provided by bird song learning, in which basal ganglia circuits induce state-dependent variability for the purposes of motor exploration during learning[19].

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 manifested? Does an Olympic basketball player just jump higher and throw more accurately than a non-athlete 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 be acquired only through practise. Indeed, one can consider any skilled professional as a person who has had the motivation to practise one thing far more (for approximately 10,000 hours extended over more than 10 years[20]) than most people could endure (BOXES 2,3). Across a wide range of tasks, the relationship between one measure of skill, the speed of task completion and the number of practise trials is well approximated by a power law[21] (FIG. 1). This implies that performance continues to improve with task-relevant practise 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 that reported performance of an industrial cigar rolling task[22]. The study included workers who had produced in excess of ten million cigars over seven years of work and 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 focused on error-based learning using adaptation paradigms, for example force fields or visuomotor rotations[23,24]. However, the link between adaptation and genuine skill development is questionable. For example, the adaptation of a single-arm reaching movement, which occurs when previously unencountered forces are experienced, is retained only partially when the same movement must be made in a bimanual reaching context[25]. This may have implications for athletic training regimens that assume skill transfer, such as single-arm swimming. Moreover, the precise roles of explicit awareness, attention, motivation and reward in 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 that is required for high achievement in sport. This can be understood intuitively by imagining oneself attempting to avoid adaptation to the wearing of prism glasses; this would not be possible as adaptation to compensate reaching errors would occur regardless of one's efforts to avoid it. Indeed, in a recent study of rotation adaptation, the forward model was learnt at the expense of the goal of the task[26]. For learning motor skills, by contrast, explicit awareness of what is required[27], attention and motivation may all be essential components. The framework that is most likely to be applicable to skill acquisition is reinforcement learning (for example, see REF. 28). The two most important characteristics of reinforcement learning are trial-and-error search and learning in the face of delayed reward. Three important sub-elements of reinforcement learning are a policy, a reward function and a value function.

This framework is immediately intuitive in relation to sports, in which 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. 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 future rewards (value). Indeed, reinforcement learning theory has an actor–critic architecture that directly parallels the player–coach dichotomy[29]. 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 own[30]. More recent reinforcement models include a fourth element, planning, through simulation of the environment (essentially this is the same as the aforementioned forward model). A skilled athlete could be considered a person who has learnt 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 learnt an accurate forward model of their arm, their racket and even of the actions of their

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

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

Prism glasses
Lenses that distort the visual input received by the eyes, typically displacing it by a set amount.

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

Reward function
The relationship between a given state and its associated reward.

Value function
The total amount of reward over current and all future states.

Actor–critic architecture
A reinforcement learning model in which the policy structure (the actor) is separate from the value function (the critic).

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

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 practise is just as applicable to cognitive activities (such as chess and language use) 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 tuning[33] and alteration in the temporal response characteristic of neurons[34]. Interestingly, these changes at early cortical stages of information processing seem to be under top-down control. Hence, an experienced athlete might more efficiently bring attentional resources to bear on those stimulus attributes that are most important for low-level processing. This was demonstrated in players of action video games, who were found to have greater selective visual attention than non-players[35]. However, evidence for improved general attentional abilities in athletes is mixed[36,37], in contrast to that pertaining to their 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 that are similar to those seen in the primary visual cortex (V1) during perceptual learning. For example, in rats, skill-related increases in cortical map representation have been reported, along with increases in the number of synapses per neuron in layer V of M1 (REF. 38). In monkeys, long-term practise of a specific reaching sequence over years is reflected in the activity of specific neurons in M1 (REF. 39), and in humans TMS and functional imaging have revealed changes in M1 representation associated with repetition of simple thumb movements[40] and with skilled sequential finger movements[41].

In cognitive psychology, theoretical descriptions of changes in skilled performance have tended to follow the pattern described by Fitts: cognitive to associative to automatic processing[42]. The key concept is that of increasing automaticity: controlled processes are attention demanding, conscious and inefficient, whereas automatic processes are rapid, smooth, effortless, demand little attentional capacity and are difficult to consciously disrupt[43]. There is evidence from dual-task experiments that novice hockey players, footballers and golfers are affected strongly by concurrent tasks (for example, monitoring a sequence of tones for a target), whereas experts show relative immunity, suggesting highly automatic performance[44,45]. Indeed, experts can struggle when they are forced to analyse their actions (BOX 4).

Crucially, it is not automaticity *per se* that is indicative of high proficiency but rather 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 of skill that we find enjoyable rather than continuing to improve our skills[46]. Hence, automaticity is more a false ceiling than a measure of excellence. Here we instead consider that motor execution skill can be more usefully defined as the ability to defy the speed–accuracy trade-off for a given task. In other words, a skilled tennis player can serve both faster and more accurately than a novice. 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 the learning of a new skill by training enhanced skill acquisition (defined as a change in the speed–accuracy trade-off function) over multiple days by having an effect on between-day consolidation[47]. Interestingly, tDCS did not affect the rate of learning in a day or the retention of motor learning over a 3-month period after training. This study supports the idea that M1 has 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 practise might have implications for professional athletics.

Expert and novice brains. A small number of studies have looked for structural and physiological differences between novice and expert athletes. TMS can be used to assess expert–novice differences by mapping-out the hand muscle representation in M1 (REF. 48). Compared with recreational players and non-players, elite racquet sport athletes show asymmetries in the motor maps of

Box 2 | **Motivation**

Motivation relates action outcomes and their utilities[112]. 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 movement[113], 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 that might be best resolved through the presence of a coach.

Motivation may improve motor performance through two effects: a general arousing or energizing effect, and a more goal-specific component[112]. An example of the latter is the observation that monkeys make faster and less variable saccades to those targets associated with the most reward[114]. 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 actions[115], but only recently has it been shown to be relevant to the trial-to-trial learning of a single action, such as a tennis return[116].

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 practise required to achieve elite status. There is evidence to suggest that those who practise the most enjoy it the least[20], which might reflect their awareness of the real goal of practise: to get better at what you are doing rather than enjoy it through the experience of short-term reward. 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 polarized history[117,118]. One position considers all skilled performance, including the elite, to be a monotonic function of the quantity of prior deliberate practise[20,46,119]. Deliberate practise is distinct from work (performance at maximal levels) and play (inherently enjoyable skill-related activities). It depends on concentration, optimized training strategies and feedback. The ability to engage in deliberate practise is constrained by resources, the requirement for recuperation and motivation.

Investigations reconstructing the practise histories of high achievers support the deliberate practise framework. Internationally competitive athletes engage in deliberate practise from an early age, and differ from national and regional competitors in accumulated hours of practise[120–123]. Training certainly dramatically influences sports-relevant physiological attributes[124–127]. However, retrospective practise histories have questionable validity, and autobiographical data yield different interpretations[128,129]. Furthermore, the study of high achievers does not take into account individuals who may have practised to little avail, and cannot establish the causal direction of the practise–attainment relationship[130].

Even in groups showing similar attainment, retrospective studies show individual differences in accumulated practise[121]. 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 VO_{2max} and strength have a genetic component[131,132], but heritability coefficient estimates depend on the environmental range under study[133], challenging generalization to elite groups[46]. Furthermore, careful monitoring of conformity to training is necessary to preclude motivational explanations[46].

What about genetic polymorphisms with known physiological actions? Many genes are of potential relevance[134–136]. For example the celebrated Finnish cross-country skier and triple-Olympic champion, Eero Mäntyranta, possesses a favourable mutation in the gene encoding the erythropoietin receptor that increases his haemoglobin concentration and consequently promotes enhanced oxygen supply to the brain and muscles[137]. In general, however, more research is needed to clarify how genes and the environment affect sporting success[138,139].

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 imagery[50]. This demonstrates a task-specific, practise-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 the integrity of the corpus callosum, assessed in humans using diffusion tractogrophy, correlate with inter-individual differences in the skill of a bimanual coordination task[51]. This result supports the idea that skilled performance can be reflected in macro-structural change. That inter-individual differences in the ability to acquire a skill might be partly attributable to genetic variations was suggested by a study showing decreased skill-learning capacity in subjects carrying a polymorphism in the gene encoding the brain-derived neurotrophic factor[52]. 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 improvement[53–55]. However, the relative importance of genetic variation in skill development remains controversial (BOX 3).

Corticospinal facilitation
Increased excitability of the corticospinal tract, measured using motor-evoked potentials.

VO_{2max}
A measure of aerobic capacity: The maximum volume of oxygen that can be used in one minute of exhaustive exercise.

Structural and functional imaging studies have also looked at patterns of change within individuals across periods of training on motor tasks. The differences found here are unambiguously the product of training (whereas expert–novice differences might instead reflect innate predispositions). However, 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 carried out by the same group[56,57]. Such structural growth might reflect an increase in cell size, the growth of new neurons or glial cells, or perhaps even an increase in spine density[58], but it seems to reverse when practise ends despite performance levels remaining elevated[57]. This reversion pattern 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 muscles[59].

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 (presumably related to controlled processing early in the progression predicted by Fitts) in so called 'scaffolding' areas, including the 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 the primary motor cortex and cerebellum[60]. Differences between expert and novice athletes have also been investigated, but the movement requirements of many sports pose certain limitations. 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 with novices, but novices' brains show more overall activity, particularly in the basal ganglia and limbic areas[61]. 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 (for example, see REF. 62) and may even predict their best performance. For example, sensorimotor event-related desynchronization in the alpha band is reduced immediately before accurate golf strokes by expert golfers when compared with their inaccurate strokes[63]. Clearly expert and novice athletes 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

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

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.

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 (reviewed recently in REFS 64,65) are beyond the scope of this Review. Suffice it to say that areas in the medial frontal cortex and the basal ganglia seem to evaluate both reward and effort costs associated with actions, and can discriminate between conflicting potential actions to opt for the most adequate in a given context. These areas consequently supervise the areas that control 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.

Experiments show that people are able to implicitly estimate the extent of their own variable error in executing a planned movement and use this estimate to modify their movements in relation to the reward context[66,67]. In one experiment, subjects jabbed at targets on a screen. Regions of the screen could yield rewards or penalties of various magnitudes, and the precise layout of these regions could be used to predict an optimal target location (in terms of maximizing payouts). For some layouts, the optimal choice location 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 response thresholds, which would then trigger the specification of an appropriate action[68–70]. However, one recent neural-network model, building on single-cell data in primates that showed simultaneous activity for different potential reaching directions[71], posits that decision making and motor preparation proceed in parallel[2] (FIG. 2). Motor plans, represented by distributions of neural activity across a population of cells[72], are generated for the most relevant actions afforded by the current environment. These motor plans compete through mutual inhibitory connections to generate a winner; this competition represents the decision process, with biasing signals from regions such as the prefrontal 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 constrained[73]. The model also explains various behavioural effects, such as the manner in which reaching movements are sometimes initially directed towards the centre of two targets[74]; 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, however, this solution offers a speed advantage as it allows the brain to begin to prepare an action before the arrival of full information. By specifying actions in parallel, the brain can 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 not enough time to wait for full specification[74]. 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 specify movements in a manner that 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 example[65]. Stimulating the frontal eye fields at different moments after the onset of stimulus triggers a saccade that deviates increasingly towards the most likely response, seemingly reflecting the evolution of an analogue decision variable[77]. Hence, motor programming and choice seem to evolve in parallel. Furthermore, spike rates in the lateral intraparietal

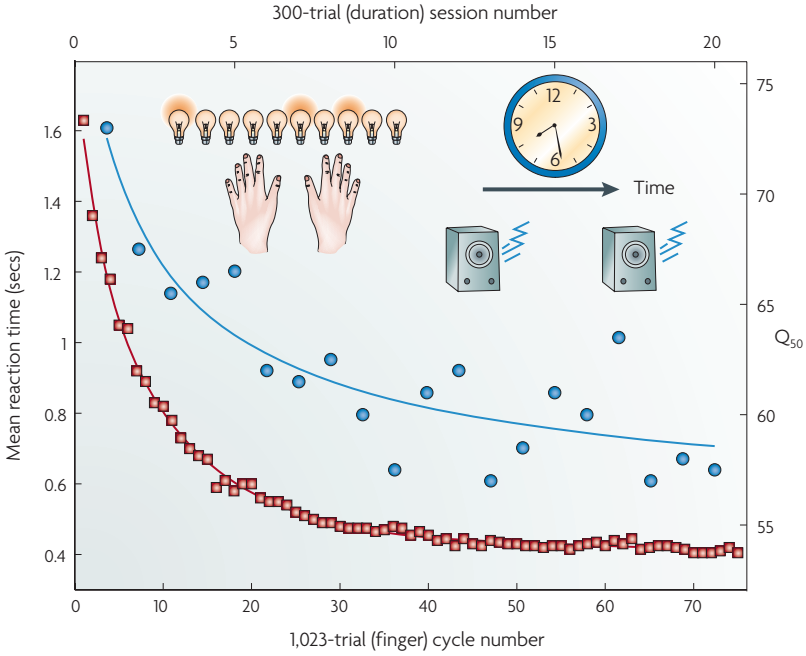


Figure 1 | **The learning curve for skill acquisition.** Example learning curves from single subjects practising over extended periods. The red data come from a choice reaction time task with 1,023 alternatives (comprising all possible patterns available to 10 fingers). Each cycle includes one repetition 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 categorized as either short or long. Q_{50} is a threshold measure, similar to the just noticeable difference, but normalized 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, whereas C reflects asymptotic performance and E is included to reflect prior learning[149]. Similar functions have dealt well with data sets in which response time is used to assess performance[21], but the precise form of the learning function remains controversial[150], as indeed does the idea that a single function (which may imply a single process) accounts for the entire learning curve[151]. Data from REFS 149,152.

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 progression pattern in skill development predicted by Fitts[42]. Highly practised skills become automatic, so performance may actually be damaged by introspection, which is characteristic of an earlier, consciously-mediated stage[142]. Experimental interventions that focus attention on movements rather than external events seem to damage the performance only of accomplished participants[143]. Anatomically, the left dorsal prefrontal cortex and right anterior cingulate cortex are activated when subjects re-attend to their movements following motor-sequence training[144]. The ability to maintain an appropriate focus might also reflect activity in the rostral prefrontal cortex, which has been implicated in shifting between stimulus-independent and stimulus-oriented modes of thought[145].

Intensive training is also associated with more debilitating conditions, including the overtraining syndrome or burn-out[146]. In some individuals repeated performance is also associated with paradoxical derangement of intensively practised movement, which may over time pervert other movements of the limb. Sustained sensory input related to the practised movements is thought to lead to abnormal plastic change in the basal ganglia and sensorimotor cortical areas[147]. Among sportspeople, such focal dystonia is best known as the 'yips' in golfers, but may also affect elite runners, tennis players and even pétanque players[148]. Once affected, individuals are usually forced to abandon professional sport.

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 variable[80]. Accumulating activity in frontal eye field motor neurons also predicts motor decisions, as shown recently using a visual search task[81].

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 that of 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 (FIG. 3a,b). 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 before 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 that of ball release[85]. Differences in information pick-up are found between novice and skilled cricketers, but also between skilled and elite players[85]. The use of advance information has mostly been assessed using first-person still and video stimuli, but is also found in real batting practise using occluding liquid crystal glasses[86]. Finally, eye movements recorded when batsmen face a bowling machine demonstrate the continued use of information after ball release[87]. 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 sports[88–92]. How is the relevant information used by experts to facilitate their performance? Anticipatory information pick-up 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 recognizable 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 actually comes from chess. Expert chess players can rapidly recognize 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 sports[95]. Although recent research has suggested an advantage for expert sportspeople over novices on some non-specific 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.

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

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

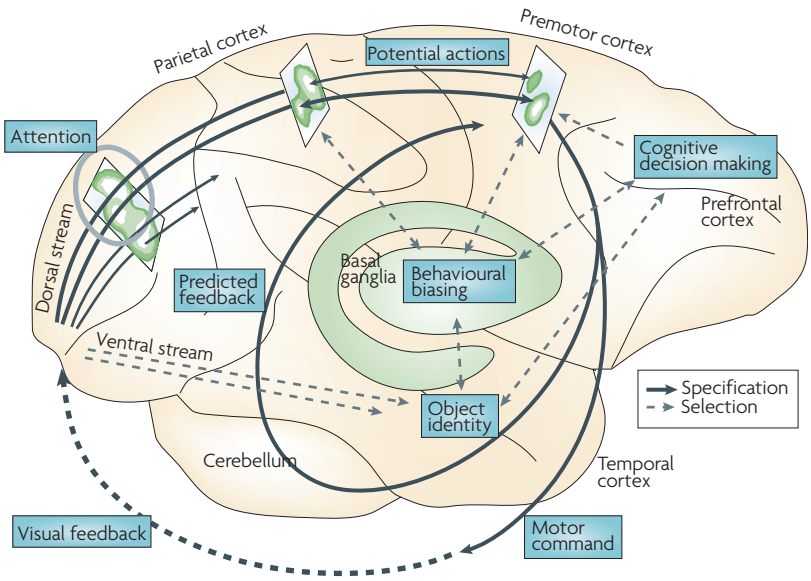


Figure 2 | **Neural substrates of the affordance competition model.** Possible neural substrates for a model of parallel motor preparation and decision making based on biased competitive interactions[2]. The model is depicted against the backdrop of a primate brain. Black arrows indicate how information arriving at the 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 frontoparietal 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 (grey 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 (dotted black arrow) and an internal prediction about feedback via a cerebellar loop (see also BOX 1). Figure is modified, with permission, from REF. 153 © (2007) Royal Society of London.

action before ball release[92] (FIG. 3c). 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 — the observing elite player had increased M1 excitability only for those hand muscles pertinent to ball throwing before the ball left the hand of the player being watched 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 that observation of action increases activation in motor areas suggests that some form of motor command that mirrors the observed action can be sent to a forward model. This supports earlier work on behaviour, showing that people can best predict subsequent trajectories from temporally occluded videos of dart throws when the videos are of their own movements[97], that is, when they already have sets of motor commands that parallel the observed action sequence. The existence of a human mirror system, which implies an automatic action simulation capability that is activated without the need to actually perform the action, has been posited in numerous studies[98–100]. 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. Indeed, 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 hand[101]. The mirror system could also have an important role in observational learning, which occurs frequently in sports coaching settings[102].

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 with similar actions with which they were not familiar, and subsequent work using gender-specific ballet moves showed that this heightened activation was dependent on motor, not visual expertise[103,104].

Third, the model of parallel interactive behaviour, along with single-unit evidence, 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 practise 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 learnt and how it is acquired 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

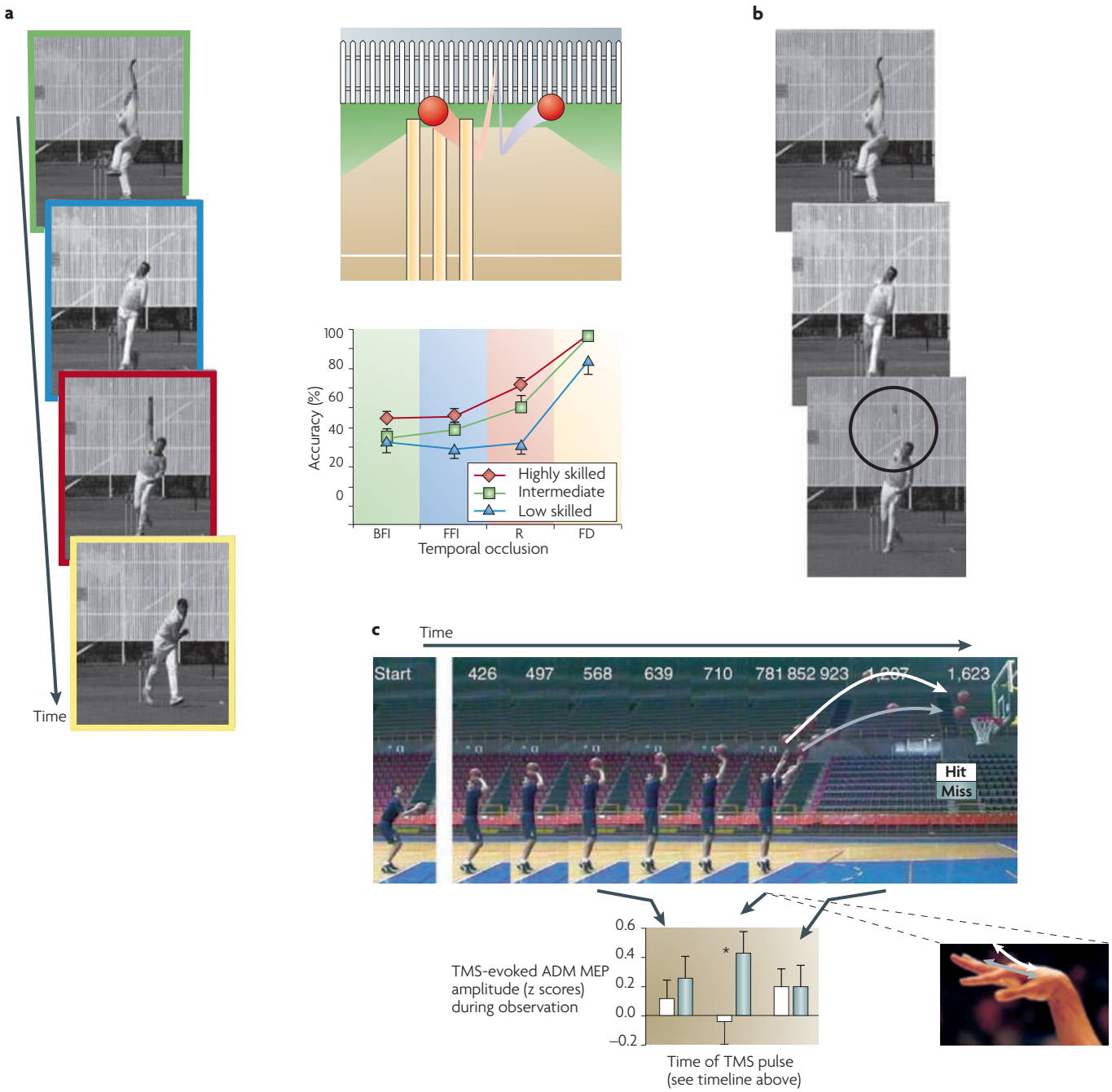


Figure 3 | **Anticipatory information pickup by expert athletes.** **a** | Schematic representation of temporal occlusion methods alongside representative data showing how highly skilled, intermediate, and low-skilled batsmen in cricket use kinematic information before a ball is released from a bowler's hand to anticipate its delivery. Subjects viewed projected movies of an onrushing bowler (left panels). The movie was stopped at the point of bowler back foot impact (BFI; shown in green), front foot impact (FFI; shown in blue), ball release (R; shown in red) or after the full delivery (FD; shown in yellow). The graph shows the 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 (example trajectories shown in top right panel). Highly skilled players performed better than intermediates and novices, and showed a reliable improvement when provided with information from FFI to R, taking their predictions above chance. **b** | Still image examples from complementary spatial occlusion experiments in which different parts of the bowler's body were occluded in a display that terminated at ball release. Here only the stills from the experiment in which the bowler's arm was occluded are shown. It was concluded that visualization of the bowler's arm and hand (black circle) were both 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 basketball players used advanced information better than expert observers or novices to predict shot success (data not shown). Crucially, 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. ADM, abductor digiti minimi; MEP, motor-evoked potential; TMS, transcranial magnetic stimulation. Parts **a** and **b** are modified, with permission, from REF. 85 © (2006) Academic Press. Part **c** is modified, with permission, from REF. 92 © (2008) Macmillan Publishers Ltd. all rights reserved.

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.

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On page 596 of the above article, there are mistakes in the details of references 140 and 141. These references should have read, respectively:

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.* **27**, 97–106 (2009).
141. Jordet, G. & Hartman, E. Avoidance motivation and choking under pressure in soccer penalty shootouts. *J. Sport Exerc. Psychol.* **30**, 450–457 (2008).