Skill memory: mind the ever-decreasing gap for offline processing

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Skills continue to be enhanced even once practice has ceased. Such offline improvements were for a time regarded as the sole preserve of sleep; yet, now recent work shows that they can occur within only a few seconds.

It was not so long ago that offline processing was considered the strict preserve of sleep. Improvements following practice would only develop during sleep ([1]; for a review; [2]). Subsequent work showed that improvements of similar magnitude could develop during wakefulness over the hours following the acquisition of a novel skill [3, 4]. Recently, offline improvements were shown developing within only a matter of minutes after practicing a novel skill [5]. Now, a new study, by Boenstrup and colleagues, convincingly shows that offline improvements can develop within only seconds [6]. The ever-decreasing gap necessary for offline improvements gives fresh insight not only into offline processing, but also into the nature of learning more broadly.

In the new work, human participants learnt a novel skill – learning a sequence of finger movements – whilst simultaneously having their brain rhythms recorded (with magnetoencephalography; MEG). Short, ten-second blocks of practice were interleaved with equally short intervals of rest. During practice there was little or no performance improvements. By contrast, in the rest interval between practice blocks there were substantial improvements. Individually these offline improvements were quite small, so called micro-offline improvements. However, cumulatively over the entire period of early practice these offline improvements were substantial. In fact, their cumulative total accounted for the amount of skill that would normally be attributed to practice. As a consequence, the defining characteristic of these offline improvements is not so much their small magnitude; instead, it is the speed of their development – they are ultra-fast offline improvements.

The emergence of these ultra-fast offline improvements may be due to the dissipation of fatigue during rest. During practice a skill is being acquired and simultaneously fatigue both physical and mental may be accumulating (Figure 1A). Performance can be seen as the result of the interaction between skill and fatigue: on the one hand, skill – improving performance – while, on the other hand, fatigue – impairing performance. As a consequence, during rest when fatigue dissipates the skill acquired during practice is expressed. This would explain the development of the ultra-fast offline improvements during rest.

Rather than fatigue dissipating, the ultra-fast offline improvements may develop due to skill enhancement during rest. Patterns of neuronal activity present during the formation of a skill memory are played out, or replayed, during subsequent rest (Figure 1B,[7]). These replay events

have been linked to the offline processing of memories, their consolidation, and specifically to their enhancement [8]. A curious and poorly understood feature of replay activity is that it is often a much-accelerated version of the activity during memory formation (i.e., time-compressed). Whilst the pattern of activity present during memory formation is preserved it occurs far faster during subsequent replay [9]. As a consequence, a sufficient number of replay events may occur even over a 10s interval to drive the formation of the ultra-fast offline improvements. During these 10s intervals there was a decrease in β power, which has been linked to replay [10]. Overall, replay with its accelerated pattern of firing is ideally suited to driving offline improvements over short intervals, and a marker of replay (i.e., a β power decrease) occurs during these intervals. Together, these findings converge to make replay a potential candidate for creating ultra-fast offline improvements.

Another possibility is that ultra-fast offline improvements emerge due to the loss of an inhibitory drive during the short rest intervals. An inhibition within the motor cortex prevents the development of offline improvements over the subsequent hours of wakefulness [11]. When this inhibition is removed, offline improvements develop over wakefulness (Figure 1C). The ultra-fast offline improvements may similarly be associated with a decrease in inhibition: they are inversely correlated with a measure of inhibition – β power. As a consequence ultra-fast offline improvements emerge as this inhibitory measure decreases, which demonstrates that the removal of an inhibitory drive may, at least in part, be responsible for the development of ultra-fast offline improvements during rest.

These various scenarios explain the emergence of ultra-fast offline improvements. However, they are not mutually exclusive. Each could make a contribution to ultra-fast offline improvements developing. In fact, they could be making complementary contributions. For instance, a decrease in the inhibition of motor circuits may be necessary for replay to take place in those circuits during rest, and so critical for the subsequent development of offline improvements. As a consequence, dissecting apart, and determining the precise contributions of each of these potential mechanisms to the development of ultra-fast offline improvements is non-trivial.

Nonetheless, substantial progress could be made in determining the mechanistic basis for ultra-fast offline improvements. One experimental approach would be to disrupt neuronal activity during the 10s rests. This could be achieved in humans using either single pulses or short bursts of Transcranial Magnetic Stimulation (TMS) while a similar high temporal resolution disruption can be achieved in animals using optogenetics [12, 13]. Disrupting neural activity would prevent replay, or other processes driving plastic changes within brain circuits, and so prevent ultra-fast improvements from developing. By contrast, the dissipation of fatigue would continue to allow the emergence of ultra-fast offline improvements despite the disruption to neuronal activity. Thus, a simple experimental approach can determine the contributions of different mechanisms to ultra-fast offline improvements.

The same basic mechanisms have been proposed to support a diverse range of offline improvements. On occasion, offline improvements are state-dependent: only developing over sleep, or having different qualitative properties depending on whether they develop over sleep or wakefulness [1, 14]; while, on other occasions, they develop over hours, minutes, or even, as elegantly demonstrated in the new study, in as little as a few seconds [3, 5, 6]. Yet, in biology, the same simple rules, or mechanisms can give rise to an enormous diversity; for example, in the pattern and shape of limbs, and this same principle, may also apply to offline processing, and more broadly behaviour [15, 16].

Practice leads to skill. However, at least in the new work, the skill was not acquired during practice; instead, it developed during the intervening period of rest. Acquiring skill predominately through offline mechanisms may alter its properties, and consequently, explain the greater skill retained following interleaved, as opposed to, a single block, of practice, when skill is acquired 'online' during practice [17]. However, skill may not ever be acquired during practice.

Skill may always be acquired following practice. Practice may trigger a set of offline process, which seconds later, lead to the acquisition of skill. Rather than occurring during practice, skill learning occurs several seconds after practice. Learning lags practice and so occurs offline after practice has ceased. This lag may be the inevitable consequence of implementing learning within a biological substrate, dependent upon time-consuming processes such as, protein synthesis [18]. Until now lengthy blocks of practice have perhaps hidden this short temporal delay between practice and subsequent skill acquisition. The skill is acquired after practice, however, more practice is being performed, and so the skill is assumed (i.e., misattributed) to come from that subsequent practice. Only when practice is massively extended, and there is no subsequent need for offline processing – with prolonged practice a skill memory does not require subsequent offline stabilisation – does it become apparent that offline processing is occurring latently during practice. [19]. By elegantly distinguishing between the contributions of practice and rest to skill acquisition, the work by Boenstrup and colleagues, have challenged the idea that skill is acquired during practice, and shown instead, that much, if not all, our skill is acquired offline during rest [6].

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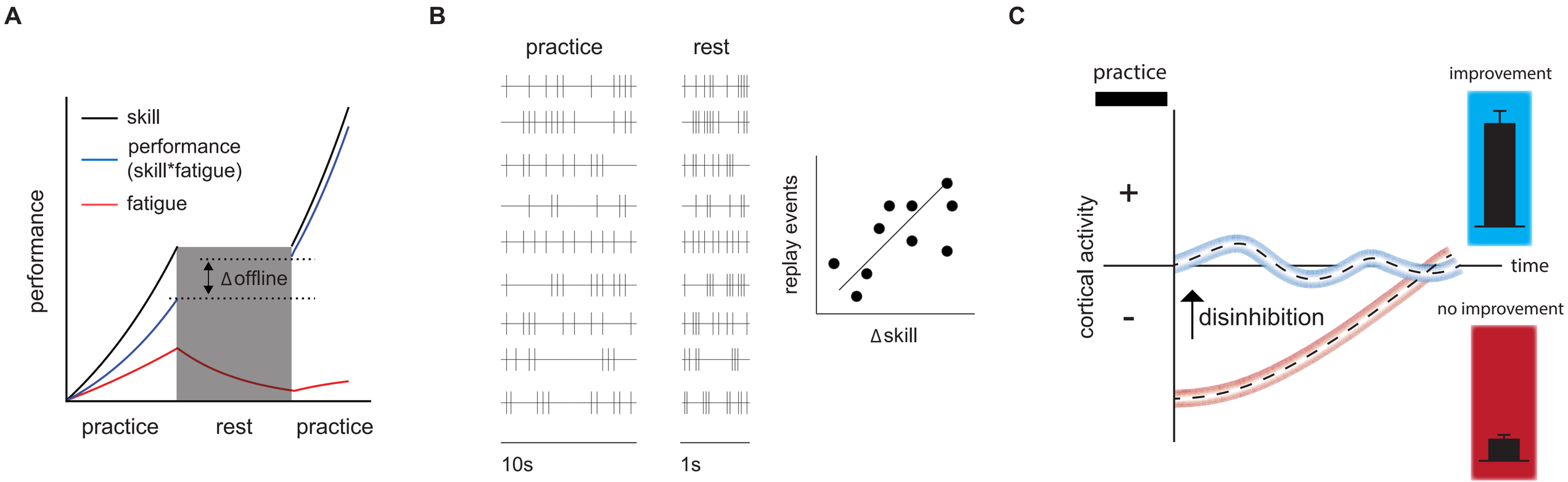
Figure Legend

Figure 1, The mechanisms underlying offline improvements during rest (A) Fatigue and skill are acquired during learning, combining together to determine performance. Fatigue dissipates during rest, which allows a greater proportion of the skill acquired during learning to be expressed. As a consequence, there is an improved performance during rest, which gives an offline improvement (Δ offline). (B) The patterns of neural activity present during memory formation emerge spontaneously during subsequent rest – albeit frequently at a faster rate – and these replay events have been linked to the development of offline improvements [7, 8]. How replay leads to the development of offline improvements, or causes other forms of offline memory processing is poorly understood. (C) Motor circuits following learning are inhibited preventing subsequent offline improvements. Conversely, the removal of this inhibition allows the development of offline improvements [11, 20]. Similarly, in the new study, a decrease in cortical inhibition – measured, as a reduction in β power – was associated with the development of ultra-fast offline improvement during rest [6]. Together, these converging studies highlight the importance of removing inhibition for the subsequent development of offline improvements.


A
skill
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Δskill
C
practice
improvement
+
cortical activity
time
-
disinhibition
no improvement