Not moving: the fundamental but neglected motor function

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The function of the motor system in preventing rather than initiating movement is often overlooked. Not only are its highest levels predominantly, and tonically, inhibitory, but in general behaviour it is often intermittent, characterized by relatively short periods of activity separated by longer periods of stillness: for most of the time we are not moving, but stationary. Furthermore, these periods of immobility are not a matter of inhibition and relaxation, but require us to expend almost as much energy as when we move, and they make just as many demands on the central nervous system in controlling their performance. The mechanisms that stop movement and maintain immobility have been a greatly neglected area of the study of the brain. This paper introduces the topics to be examined in this special issue of Philosophical Transactions, discussing the various types of stopping and stillness, the problems that they impose on the motor system, the kinds of neural mechanism that underlie them and how they can go wrong.

This article is part of the themed issue 'Movement suppression: brain mechanisms for stopping and stillness'.

1. Introduction: the elephant in the room

It is natural to imagine that the motor system exists so that we may move. Yet we only have to look at animals or people going about their normal business to realize that they are more often stationary than in motion. The squirrel crossing our lawn darts frenetically from one position to the next, but in between adopts a rigidly statue-like pose of utterly suspended animation. Our eyes generate saccades—eye movements that jump with remarkable speed from one visual object to another in the visual field—that are separated by relatively long periods of virtually complete immobility. In a similar way, Escherichia coli progresses by an alternation between rapid propulsion to a new position, followed by a pause during which it decides to set off in a new direction, creating paths that are remarkably similar to those traced about by the human eye in visual scanning (figure 1): both are foraging—E. coli for nourishment, our eyes for information. And like our eyes, our hands perpetually alternate between reaching and grasping [3].

The fact that the motor system is as much concerned with not moving as with moving has always been something of an elephant in the room. As Sherrington wrote in 1915: 'The role of muscle as an executant of movements is so striking that its office in preventing movement and displacement is somewhat overlooked' [4]. Furthermore, we shall see that the maintenance of stillness is not simply a matter of doing nothing: it requires as much if not more active and accurate control as creating the movements themselves.

2. Decisions, hierarchies and descending inhibition

This pervasive stillness is reflected in the prevalence of inhibitory rather than excitatory processes at the highest levels of the motor system. The output of the cerebellar cortex, for instance, is entirely inhibitory; the control of saccades is partly through a series of descending inhibitory projections from the basal
ganglia to the superior colliculus [5]; and even in the most primitive brains—the Tiger Salamander’s, for example—the very highest levels such as the habenula are tonically inhibitory and work by local disinhibition [6]. This apparently fundamental motor plan can be regarded as a necessary consequence of the fact that the motor system, like any organization intended to generate detailed and complex patterns of output—a business, a computer or, archetypically, an army—is arranged hierarchically [7]. This analogy between neural and military organization was noted some five centuries ago by Leonardo da Vinci: ‘I nervi, coi loro muscoli, servono alle corde, come i soldati a condottieri, e le corde servano al senso comune, come i condottieri al capitano’. [8, pp. Fogli, B, 2 recto] (The nerves and muscles serve the cord as soldiers do the lieutenants, and the cord serves the brain as the lieutenants do the commander.) In such hierarchies, the functions of the units at each level are very different. At the bottom, individual soldiers can respond quickly to threats or opportunities immediately in front of them, but lack the kind of wide-ranging information that is needed to make strategic decisions, and is only available to those at the top. Consequently, there may often be conflict between local decisions and more global ones. The descending flow of command must therefore be at least as much negative—to prevent short-sighted responses—as positive.

A telling indicator of this, seldom remarked upon, is the embarrassing contrast between the weapons issued to officers and those issued to their men during the trench warfare of the past century: the men have rifles or other weapons designed to harm the enemy, whereas the officer’s weapon is the pistol—not primarily intended for the enemy at all, but needed to inhibit his men from doing what their instincts would naturally suggest. And as Gordon Holmes once pointed out, the same principle of descending inhibition underlies the common bicameral organization of legislative assemblies: ‘…modern work has emphasised that (cortical areas) are largely concerned in keeping subcortical activities under proper control. The higher centres can be, in fact, compared to the second chamber of a legislature which is capable of action on its own, but its chief function is to prevent an assembly representative of many and diverse interests, but less well informed of all the bearings and facts of the situation and, therefore, less discriminative, from reacting to every impulse of the moment’ [9, p. 575]. Even the simplest organism is faced at every moment with an almost infinite number of hypothetical things it might do. The default must therefore be global inhibition, with actions being selected by disinhibition.

A particularly clear example of tonic descending inhibition occurs in the control of saccades, where there is a hierarchy of at least two levels. At the bottom, the superior colliculus, receiving information from the visual system and projecting downwards to the neurons in the brainstem that generate saccades to designated locations in space, provides an elegant neural mechanism that translates the position of activity on its topographically arranged map of the visual world to an appropriate command to generate a saccade to look at it [10] (figure 2a). If our world consisted of nothing but single LED targets in a darkened room, this would work beautifully and saccades would be made accurately and automatically to fixate them. But in practice we are surrounded by very many possible targets, some more important than others—perhaps more mysterious or threatening. The simple collicular mechanism cannot cope with this situation, not just because it has no way of dealing with multiple targets, but more fundamentally because it is too ignorant: it knows where things are, but has no idea what they are. So it cannot be allowed to decide what to look at: only higher levels of the brain—cortex, and descending evaluatory pathways through the basal ganglia—can make judgments about the relative need to examine one part of the visual world rather than another. Such judgments necessarily take time, whereas the colliculus is fast: in principle it should be capable of generating a saccade within some 60 ms of the appearance of a visual target, whereas visually driven saccades normally take something nearer 200 ms.

Decisions have to take a long time. Even at rest, we are remorselessly expending energy; if we do not replenish it, we die. But unless—like a sea-anemone—we dwell in one of those delicious environments where food comes to us rather than us going to it, we have to weigh the metabolic cost of moving against the likely metabolic benefit from ingesting our prey. So we are in the same position as a company that must decide whether to make a costly investment in the hope of getting more in return. It is not surprising that the very highest parts of the brain are dedicated to what is ultimately its single most important function and raison d’être, nor that decisions take so long to be made. Reaction times are in general much longer than one might calculate from the shortest routes linking stimuli to responses: this procrastination reflects the immensely greater complexity required to make these evaluations, compared with simple and local low-level responses. They are also necessarily probabilistic, for all we can ever do is choose the action that seems to us most likely to achieve a desired result: the all-pervasive noise in the outside world, combined with the uncertainty of sensory stimuli, means that these decisions are sometimes successful and sometimes not. As in business, and as in war, they represent gambles [11,12].
Deciding to stop an ongoing movement requires, in general, internal models of almost equal complexity. A particularly clear example is the control of drinking [13,14]. Thirst, combined with opportunity, is sufficient to initiate drinking: but to determine when to stop is not so easy. Although the ultimate aim—the correct degree of bodily hydration—is obvious enough, the problem is that there is a very long lag before the effects of ingesting a given amount of water result in a new equilibrium: if we only stopped drinking when the desired set point was actually reached, we would die of over-hydration. Thus, even for this extremely basic physiological function the brain must have a model of the dynamic properties of the blood and tissues in response to a given intake of fluid, and predict the right moment to stop, which will ultimately result in the desired state. On a much shorter timescale, the same problem arises whenever we attempt a precise movement when feedback is only available after a delay. A good example, discussed by Optican and Pretegiana in this issue [15], is the control of saccades; the movement is so fast, and visual feedback so slow, that we cannot simply stop moving the eye when we see that the visual target has been achieved, for this will result in gross overshoot. The oculomotor system has to construct an internal model of the mechanics of the eye, operating in real time, that halts the eye at the correct moment [16,17].

Thanks to intensive behavioural and neurophysiological work over the last decades, there is wide agreement about the neural mechanisms that actually make decisions. The general process appears to be one of accumulation of sensory evidence, leading to rising decision signals that compete with one another in a kind of race [18–21]. Whichever reaches threshold first ‘wins’, in the sense of initiating a corresponding response. What is attractive about cumulative mechanisms of this kind is that with suitable assumptions they also embody a kind of Bayesian mechanism, which ought in principle to be the most efficient way of making a decision in the face of uncertainty either about the incoming information, or—as is more often the case—about the possible consequences of a response. This cumulation can be observed directly by analysing reaction times (latencies) in experiments in which a human or animal subject is required to respond as rapidly as possible to a suddenly presented stimulus. Because of the random variability mentioned above, even with a single stimulus the latency varies randomly from trial to trial, and a cumulative histogram of the number of responses as a function of latency, when plotted on appropriate axes (a reciprocit plot: figure 3), shows a cumulative function whose characteristics are directly related to those of the underlying neural process [22]. In accordance with a Bayesian interpretation of this mechanism, as provided for instance by the LATER model [23,24], manipulation of prior probability, of the rate of supply of information or of the threshold criterion for a response all result in exactly the alterations of the plot that would be predicted on theoretical grounds [25,26]. Deciding between alternative actions would then be implemented by running a race between two such cumulative processes, the one reaching threshold first determining what action is finally performed [27]. But such a mechanism cannot be strictly Bayesian. If it were, it would be liable—like Buridan’s ass, equidistant from two equally attractive bales of hay—to starve in the midst of plenty; there must be some randomising mechanism for tie-breaking, with the added benefit that randomness will render our actions unpredictable—an advantage both for predators and prey [28]. God may not play dice [29], but our brains do [30].

The relevance of all this to stopping is that we can see what happens to the distributions when we make unexpected modifications of the stimulus, such as suddenly cuing the subject not to make the response after all, or presenting a new alternative stimulus. Such experiments are doubly valuable: not only do they shed light on the neural mechanisms of stopping, but they provide a tool for investigating the cumulative process itself. In figure 3, for instance, we see what happens in a countermanding experiment [31–33], where, on some trials in a conventional step task, the central fixation target reappears after a short delay—in this case 100 ms—and the subject has been told that if this stop signal occurs they are to suppress the movement they would otherwise make. Sometimes they are successful, sometimes not; as would be expected, the longer the delay, the less often they succeed in cancelling the action in time. It is obvious in figure 3 that the cumulation of responses begins in exactly the same way in control and countermanding trials, but in countermanding trials the cumulation ceases prematurely, in this case at 72%, representing the proportion of trials in which countermanding is unsuccessful. This behaviour can be exactly modelled
by supposing that there is a race between two LATER-like units, a Go unit that initiates the movement, and a Stop unit, driven by the stop signal, that acts to suppress the Go unit and thus causes countermanding to occur. Because of the intrinsic randomness of these two processes, for a given delay the Stop unit will sometimes successfully inhibit the Go unit before the latter can initiate the movement, and sometimes not. The details of such a model, and of several others that can explain other kinds of stopping experiments, are described in Noorani’s contribution to this issue [34].

Perhaps some apology is needed for what may seem an overemphasis on eye movements. The fact is that we know much more about eye movements and their control by the brain than any other aspect of the motor system. The reason is partly that the output of the oculomotor system is relatively simple (with only three degrees of freedom for each eye), and relatively easy to measure both quickly and accurately; in addition, it is a system with a well-defined input (primarily visual and vestibular, with some additional mechanoreceptor information). Correspondingly, the underlying neural circuits are relatively well-defined and have been very thoroughly investigated, with a tradition of precise quantitative analysis that is largely due to the pioneering work of David Robinson, originally trained as an engineer [35–37], that has proved much more difficult to achieve in other areas of the motor system; David sadly passed away in October 2016, and will be deeply missed—without him, the oculomotor landscape would have been utterly different.

The oculomotor system is in effect a microcosm of the brain itself [38]; as Sherrington presciently wrote in Man on his Nature, ‘An act which may seem simple even to banality is the directing of the gaze. Yet its factors engage the roof-brain far and wide . . .’ [39, p. 225]. In addition, saccades in particular are stereotyped, essentially unconscious and extremely common movements. With modern recording equipment, one can measure many hundreds of saccades without fatiguing the subject. Since each saccade is in effect a decision, this has meant that much of what we know about decision processes in general has come about through examining saccadic behaviour in response to complex visual stimuli [19,20].

3. The functional types of stopping and stillness

So far we have introduced just three types of stopping: the tonic descending inhibition needed to prevent lower levels of the brain from making over-fast, unsophisticated responses to external events; and two situations in which stopping must suddenly be turned on: when an impending movement needs to be prevented, and when a movement actually in progress needs to be halted so that it will terminate exactly at the intended target. But many other varieties of stopping exist, and it is helpful to try to classify them all in a systematic way. A primary distinction is between long-term immobilization, often global in its effect, and short-term stopping of a specific movement either begun or about to begin. Secondary distinctions are mostly a matter of what triggers the stopping.

(a) Long-term, global

(i) Background, ‘default’ stopping

This is the very general phenomenon discussed above, that the large number of possible movements that could be made at any one time means that the default must be to tonically suppress all of them, and then select what is actually wanted by a mechanism of disinhibition. It also includes the descending hierarchical inhibition by which more primitive responses are suppressed in favour of more sophisticated ones. A well-known example of failure of such descending inhibition is the Babinski sign—extension rather than flexion in response to stroking the plantar surface [40]. The ‘release’ characteristic of some kinds of higher motor disorder (ballismus, athetosis) can also be regarded as a failure of tonic descending inhibition [38].

(ii) Active immobilization

Relatively long-term immobilization may also be a specific and active response to certain situations. One example is the ‘freezing’ seen in predators stalking their prey, or in the prey themselves to make them inconspicuous, or the related but shorter-lived startle response, discussed by Kreitzer in this issue [41]. As pointed out by Roelofs, also in this issue,
[42], freezing can also be a feature of certain kinds of human behavioural disorder. A more localized form of active freezing is the common protective response to injury, when, for instance, the abdominal wall becomes rigid after visceral injury or infection, or the spinal musculature generates widespread contraction to prevent further injury.

(iii) Passive immobilization
The third kind of immobilization results in a reduction in muscle tone that is typically global: it occurs cyclically in sleep, resulting in muscle relaxation and loss of posture, and pathologically in coma and of course ultimately in death; in milder form it can be observed in severe depression [43]. Both functionally and neurally it is completely distinct from the other forms of inhibition, and is not discussed in this special issue.

(b) Short-term, specific
(i) Determination of movement duration
Many movements are too fast to be controlled by immediate feedback, in other words by sensing that the goal has been reached. As mentioned earlier, a very good example is the saccade: if we relied on vision to terminate the movement, it would wildly overshoot. It must instead be ballistic, with some kind of internal mechanism determining the moment at which to stop moving; one possibility is to use internal feedback, based on the output of a real-time dynamic model of the movement in progress [44,45]. These possibilities are discussed in this issue by Optican [15]. Impairment of such a mechanism will tend to give rise to dysmetria, for instance the overshoot characteristic of cerebellar dysfunction [46].

(ii) Externally driven stopping
A common situation in the real world is when a sudden unexpected event—a ‘stop signal’—means that we must cancel an intended movement. This kind of countermanding is sometimes successful and sometimes not, depending on how quickly the stop signal occurs after the movement has been initiated, and analysis of how the distribution of reaction times is affected by when the stop signal occurs has been a fruitful source of information about the underlying decision system (see above, and figure 3). These mechanisms are discussed in detail by Pouget et al. [47] and Schall et al. [48]. Another task that on the face of it is also externally driven is the Go/No-go task, in which a subject is instructed to respond to certain types of target (red ones, for example) but not to others (e.g. of the wrong colour). However, in the sense that, right from the beginning of each trial, the system knows that it must suppress its initial response—simply to the existence of the target, irrespective of its colour—this suppression is perhaps better regarded as an example of internally driven stopping.

(iii) Internally driven stopping
There are often situations where an action must be cancelled because the brain itself has realized that it is unwanted. A good example, introduced above, is the Go/NoGo task where subjects inevitably make erroneous responses to the forbidden target; to prevent this, the system appears to initiate a process of internal cancellation that may result in successful cancellation of the first movement that is not yet properly informed as to the target’s colour (a signal that arrives later)

4. The difficulty of achieving stillness
One might well think that stopping, and maintaining stillness, was simply a matter of turning off the excitatory commands to muscles. But—apart from the special case of deep sleep, when the body simply flops passively—this is absolutely not the case. The reason is a peculiarity—in fact a defect—in the way muscles work at a molecular level. Consider the two stationary
The difficulty in achieving stillness is reflected in the very many kinds of impairment that can arise from neurological...
disorder. Gaze-evoked nystagmus has already been mentioned; other types of oscillation (the rest tremor of Parkinson's disease, the intention tremor of certain kinds of cerebellar dysfunction, essential tremor) are all likely to be due to a failure, at some level, of direct feedback. Parkinsonian perseverance, and the chorea, athetosis and ballismus of some other afflictions of the basal ganglia [72] can be thought of as a failure of tonic descending inhibition, and—at a higher level—may explain Tourette's syndrome and other examples of a high-level lack of restraint. This special issue of Philosophical Transactions is not primarily intended to address such questions, but the contribution by Jahanshahi and Rothwell [73] provides some neurological insights into this neglected area, and for clinical aspects of oculomotor disorders The Neurology of Eye Movements [74] is essential reading.

Figure 6. Integration. (a) Integration transforms a pulse command into a movement that begins and ends with stillness. (b) If the integrator is leaky, the final position cannot be maintained and will drift back to the starting position. (c) As a result, repeated efforts to attain the target will result in a kind of oscillation—in the case of eye movements, this is called gaze-evoked nystagmus. (d) An example of gaze-evoked nystagmus (after Kommerell [62]).

Figure 7. The hierarchy of keeping still. Visual information is combined first with oculomotor efference copy and then with information from the vestibular system to estimate the position and velocity of the head. This signal drives compensatory eye movements, and also combines with information about the position of the head relative to the body to estimate body position in space, which—in conjunction with knowledge of pressure distribution over the support area—results in postural commands to maintain stability; muscle spindles help ensure that these commands are correctly carried out. VOR, OKR: vestibulo-ocular and optokinetic responses. After Carpenter & Reddi [70].

5. What stillness can teach us

There is perhaps a general lesson to be learnt from all this. Typographical designers are trained to perceive the counters, the bits between the letters, often beautiful in themselves, that greatly affect the aesthetic effect of a text. In the same way, we should train ourselves to think sometimes about the spaces between phenomena rather than narrowly focusing on the phenomena themselves: fixations pose every bit as interesting a question as the saccades that separate them, not moving is often harder than moving, and stopping and stillness have much to tell us about the mysteries of such dark areas as the basal ganglia.

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