Cognitive motor control: spatial and temporal aspects

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Cognitive motor control refers to processes that blend cognitive and motor functions in a seamless, interwoven fashion. Such functions evolve in space and time at various levels of complexity. This article focuses on conceptual issues regarding spatial and temporal aspects of motor control as well as on methods suitable for extracting information from neuronal ensembles.

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Introduction

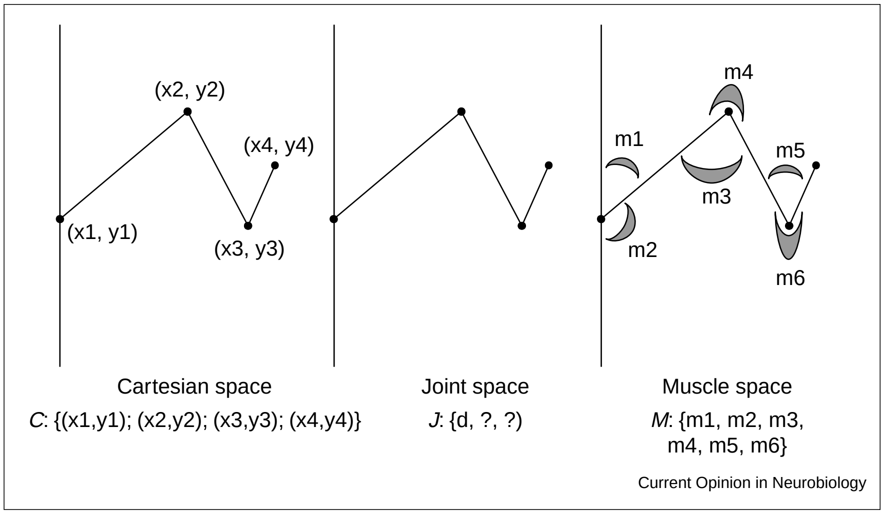
Movements possess spatio-temporal characteristics: they happen in space and evolve in time. However, spatial and temporal aspects can be dissociated and controlled separately; for example, you can draw a square in different sizes and places (spatial aspects) and at different speeds (temporal aspect). Naturally, a movement is made as a whole with apparently indivisible blends of spatio-temporal characteristics, depending on the demands of the particular task. I would like to argue that spatial and temporal aspects involve separate processes, for which general principles apply when extracting information in space and when implementing tasks in time.

Spatial aspects

Let us consider an evolving movement. Its spatial path p can be described within an arbitrary, but internally consistent, formal space Q in domain $\Re$, $Q(\Re)$. For example, in this domain of arm movements, a particular movement can be described in terms of its Cartesian coordinates, joint angles, muscle activations, etc. These descriptions hold within the respective Cartesian, $C(\Re)$, joint angle, $J(\Re)$ and muscle $M(\Re)$ formal spaces (Figure 1). By differentiating the path $p^{Q(\Re)}$ with respect to a path-parametrizing variable s, we obtain a purely spatial 'steering function', $\omega^{Q(\Re)}(s) = dp^{Q(\Re)}/ds$. This steering function denotes the direction of an infinitesimally small change (i.e. tangential vector) in $Q(\Re)$. (This expression holds for any multi-dimensional space in $\Re$.) As devices measuring motion commonly use Cartesian coordinates for convenience, movement direction is usually referred to in terms of Cartesian space $C(\Re)$ but, of course, it could be re-expressed within a different formal space, for example, a joint space $J(\Re)$ or a muscle space $M(\Re)$.

Changes in neuronal activity in practically all of the areas of the brain that have been investigated are related to the direction of movement. In addition, the direction of the weighted directional sum across the neuronal population — that is, the direction of the neuronal population vector — yields a good estimate of the direction of movement. The same information can be extracted by other more optimal methods and by non-vectorial techniques [1]. In the general case, non-directional variables can be processed and extracted [1,2]. Thus, these methods are essentially calculations that are applied to inputs to extract certain information from neuronal populations. Depending

Figure 1



Schematic diagram to illustrate three spaces (out of many possible spaces) in a hypothetical posture. Thick lines could represent linked skeleton segments (e.g. of the arm) in two dimensions. Notice that joint angles by themselves are not sufficient to specify the state of the system (the lengths of the segments are needed too); and similarly for the muscles, external loads acting on the segments need to be taken into account.

on the kind of input, the result will be different. Examples of such results might include: direction of movement as determined in motor cortex [3,4••]; spatial location during navigation as determined from neuronal activity in the hippocampus [1]; direction of bend in the leech [5]; direction of wind-evoked escape turns in the cockroach [6••]; time course of stimulus motion as determined in temporal cortex and of hand motion as determined in motor cortex [7•]; and direction of heading as determined in temporal cortex [8]. The point is that these calculations, including the neuronal population vector, do not vary according to the nature of the inputs: they are tools that can be used to decode activity in populations of neurons, and, by themselves, do not address which population characteristics are relevant; these characteristics of interest depend on the experimental design of the biological study. Thus, these methods are general-purpose, powerful tools for analysing neuronal populations.

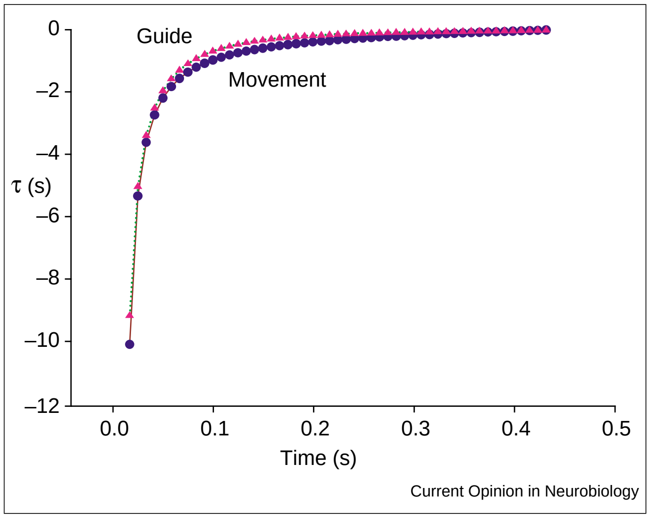
It should be noted that the population vector can be sensitive to the neural measures used as inputs [9], and care should be exercised in its application. An important point is that the behavioural inputs and neural outputs of the analysis should be congruent, otherwise they can lead to uninterpretable results [10•]. The situation is usually clearer in invertebrate systems, in which fewer neurons provide a simpler system. Remarkably, the population vector has worked well in such systems [5,6••], even when tested rigorously and compared with a strong alternative hypothesis in a controlled experiment [6••].

Temporal aspects

A dynamic, purely temporal measure of movement is indispensable in motor control. First, consider a single, one-dimensional movement (from rest to rest) in space $Q(\mathfrak{R})$. The distance to be covered by the movement can be thought of as a 'gap' to be closed; at time t the gap is $D^{Q(\mathfrak{R})}(t)$. By differentiating the trajectory with respect to time, we obtain the rate of change of position, that is, instantaneous speed: $\dot{p}^{Q(\mathfrak{R})}(t) = dp^{Q(\mathfrak{R})}/dt$. Notice that speed is not a purely temporal quantity but a composite spatio–temporal measure and, therefore, does not fulfil the criteria of our quest. Therefore, we turn to an extent of time, that is, a duration. A good measure is the variable τ [11], which is an estimate of the time taken to close the gap; its value is given by $\tau(t) = D^{Q(\mathfrak{R})}(t)/\dot{p}^{Q(\mathfrak{R})}(t)$. Although the terms in this ratio are spatio–temporal, τ itself is a duration, expressed in units of time alone. Also, notice that $\tau(t)$ is defined with respect to the time at instant t, and that it is a function of the instantaneous speed $\dot{p}^{Q(\mathfrak{R})}(t)$ and of the current gap $D^{Q(\mathfrak{R})}(t)$.

The behavioural relevance of τ was established in early studies that demonstrated that the initiation of movements for avoidance or interception depended upon a critical τ value [11]. During the past 25 years, research has focused on examining the shape of the $\tau(t)$ function across various sensory and motor behaviours (including vision, echolocation, reaching, flying, and so on) and in different species (including humans, birds and bats). These studies revealed a remarkable consistency in the shape of the $\tau(t)$ function across behaviours, conditions and species [12]. This led to the hypothesis that the temporal evolution of diverse finite biological processes (i.e. those with a beginning and an end) is governed by the same 'generalised' $\tau(t)$ function, called the τ-guide [τ_g]. This function has the form $\tau_g(t) = 0.5(t - T^2/t)$, where T is the duration of the movement and t is the elapsed time from the start of the movement ([12]; Figure 2). This equation implies a process that evolves with constant acceleration, and is derived directly from Newton's equations of motion under a constant force, such as gravity. When dealing with several processes, the coupling of separate $\tau(t)$ functions has been proposed as a mechanism to temporally coordinate those processes [12,13]: $\tau^A(t) = k\tau^B(t)$, where A and B denote two different processes, and k is a gain constant. This generalises the approach to multiple dimensions and can be extended without difficulty to sequential processes.

Figure 2



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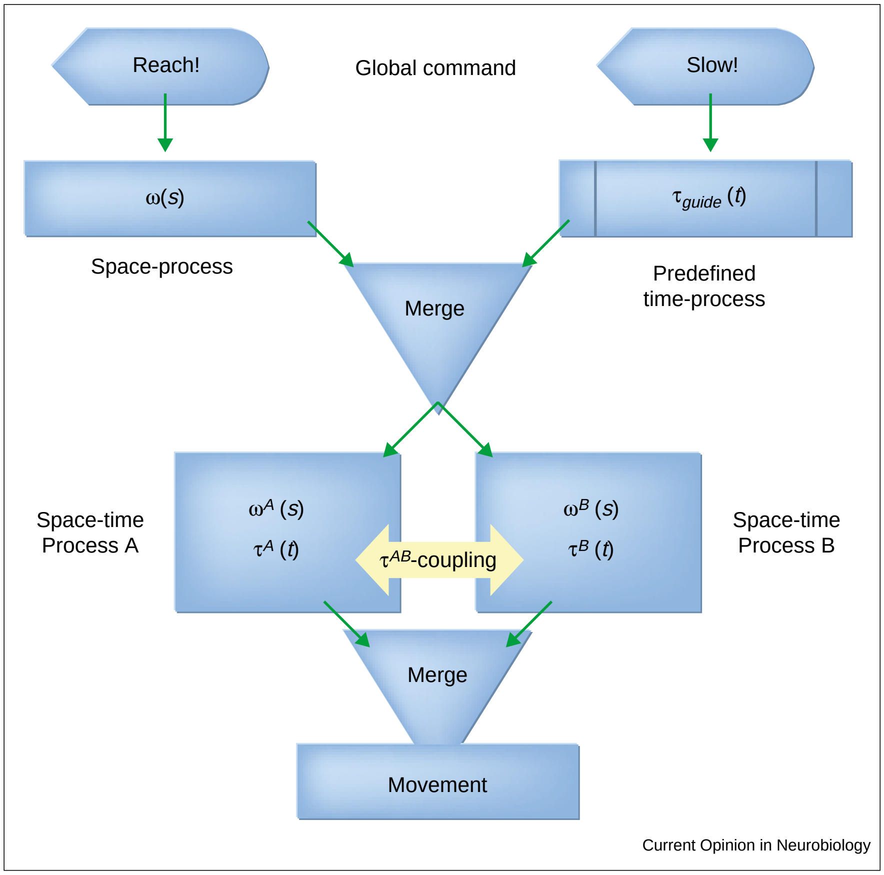
Traces of functions for $\tau_g(t)$ and $\tau(t)$ functions as indicated. Data are from a single trial of a 20cm pointing movement by a healthy subject. (Unpublished data; courtesy of MA Grealy and DN Lee.)

The $\tau(t)$ function is a general and purely temporal measure that does not depend on the specifics of a particular case. In that sense, it is qualitatively similar to the population methods discussed in the section on spatial aspects; they are both 'formal' procedures that can operate on various 'contents' (e.g. behaviours) but do not carry case-specific information. In addition, similarly to population methods, the $\tau(t)$ analysis could be applied to neural data. Consider, for example, two neuronal populations (e.g. in motor cortex and cerebellum) that are studied during reaching movements. The population-analysis methods could be used to predict the direction of movement of the two populations in space at any given instant, and to evaluate

Figure 3



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Flowchart diagram of hypothesised spatial and temporal processes. See text for details. Shapes conform to standard flowchart conventions (Figure 5).

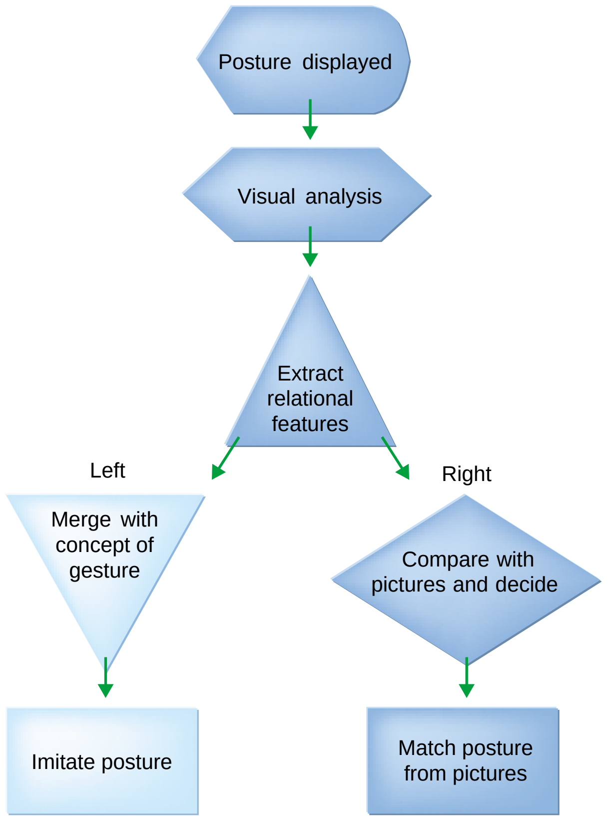
their spatial coupling. In a complementary fashion, the $\tau(t)$ analysis could be used to derive their particular $\tau(t)$ functions and to evaluate their temporal coupling.

Spatio–temporal aspects

At the behavioural level, spatial aspects of movement are usually specified globally (e.g. by the location of the target), whereas the actual movement path is left unconstrained. Similarly, detailed temporal aspects are usually left unspecified (e.g. one reaches for a cup at one's own speed), and general aspects are specified in a global way: in terms of fast or slow movement, or within an instructed duration of movement (e.g. by visual signals or a metronome). Thus, the spatial $\omega^{Q(\mathfrak{R})}(s)$ and temporal $\tau(t)$ courses are commonly left unspecified. The latter typically follows the $\tau_g(t)$ function but the former does not follow a certain pattern. Several theories have been proposed [14] as general principles to account for movement paths, but these paths may depend on task conditions [15]. This difference between the temporal and spatial courses might be due to the fact that, whereas time is a unique variable, there are many possible formal spaces. Depending on the particular task, which may include specific instructions (e.g. move in a straight line, do not move close to obstacles and so on), different spatial courses could be followed to satisfy the task-specific constraints.

These considerations point to new directions towards which studies of mechanisms of movement in the central nervous system (CNS) could be turned, especially now that simultaneous recordings from several brain areas are becoming more frequent (Figure 3). According to a current viewpoint [16•], the CNS is involved in specifying and/or controlling movement parameters. This implies a direct relation of neural activity to 'bundled' spatio–temporal signals, such as speed [17•]. Obviously, there is great need for further research on the motor/temporal domain. For example, the $\tau(t)$ function could be calculated for different areas (at the neuronal population level), and the degree and magnitude of their coupling determined. In addition, as $\tau(t)$ is a time series, powerful statistical methods that have been developed in that field could be applied to describe the internal structure of this function. Cross-correlation analysis can be used to determine the nature and time course of interactions between brain areas rigorously and quantitatively. For example, such analysis could determine which area leads or lags another, by how long, for how long, and in what direction (i.e. is the effect positive or negative), and could also be used to derive transfer function coefficients that quantify interactions between areas. These coefficients will, in fact, be coupling coefficients at various time lags. Thus, it should be possible to fully describe time-varying interactions among areas. On the

Figure 4



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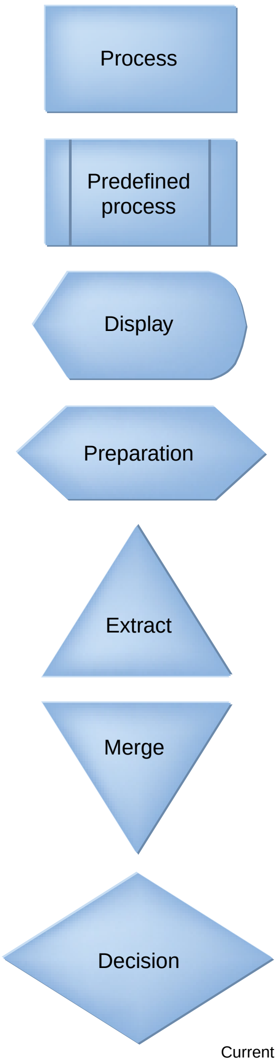
Flowchart diagram of processes that are involved in imitating and matching meaningless postures of the hand (with respect to the body). Left and right refer to hemispheres. (Inspired by [19]).

Figure 5



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Labelling of flow chart symbols.

other hand, the investigation of the neural mechanisms of purely spatial aspects of movements is more challenging because such aspects can frequently be expressed with similar internal consistency (although not simplicity!) in different formal spaces (e.g. Cartesian, joint, muscle and so on). The question of which of these spaces are operated on by CNS motor mechanisms has been a perennial preoccupation in the field; the answer is not forthcoming because these various spaces are interrelated [1,3,17•]. However, the well-documented dissociation between mechanisms that subserve learning in kinematic and dynamic (i.e. kinetic) spaces [18] points to a general segregation of the corresponding neural mechanisms.

It is also possible that different areas of the brain deal differentially with spatial and/or temporal aspects of movement. For example, motor cortex and cerebellum might indeed be multiplexed to various spatio–temporal movement parameters [16•]. On the other hand, one could attempt to remove a postulated temporal signal using statistical techniques. For example, regressing a given population-activity envelope onto $\tau_g(t)$ would allow the analysis of the residuals with respect to spatial factors in selected formal spaces. It is likely that spatial and temporal effects are distributed to various brain areas, and that particular areas of the brain could be involved in a differential and graded manner. The quest for ‘spatial’ or ‘temporal’ areas will be elusive but worth the effort.

Imitation

A lead on mechanisms that control spatial aspects of movement could be provided by research on imitating meaningless postures [19,20], as such movements are devoid of familiarity or long-term memory features. Studies of patients that have brain lesions that affect the reproduction of meaningless postures have revealed systematic differences between the two hemispheres. Lesions in the left hemisphere typically affect the imitation of hand postures with respect to the rest of the body, especially the head. By contrast, lesions in the right hemisphere typically affect imitation of postures of fingers with respect to themselves [19]. These findings led to the hypothesis that the left hemisphere is involved in higher-order 'conceptual' aspects of spatial representations of body parts, whereas the right hemisphere comes into play when more detailed perceptual discriminations of complex (but within one body part, i.e. the hand) configurations are needed ([19]; Figure 4). Such complex interactions make it unlikely that the imitation of meaningless postures is subserved by body-part specific populations of so-called 'mirror neurons' [21,22]. An additional piece of evidence against this idea comes from recent work [23••] in which imitation of postures of hand, fingers and foot were examined in a population of patients who had an infarct in the territory of the middle cerebral artery (MCA). This territory spares the dorsal portion of the premotor cortex, where foot mirror neurons are supposedly localised in the human brain [22]. Therefore, the mirror-neuron hypothesis would predict that MCA infarctions should spare imitation of foot postures but this was not the case [23••]. Although this hypothesis may be of heuristic value, the brain mechanisms that underlie the imitation of meaningless postures are more complex than the mirror-neuron hypothesis would allow for.

Moving from memory

The systematic errors in pointing after a delay [24,25•] form another fertile ground for investigating cognitive processes that are involved in purely spatial aspects of motor control. Pointing to a target within a circle after a memorised delay results in systematic errors towards the oblique axes, and away from the centre and the periphery [24]. This effect has also been studied at different stages of development [26]. The current explanation for this effect is that it reflects a categorisation of space, which comes more and more into play as the delay lengthens, that is, as the memory of the target fades. Thus, in the absence of accurate memory, categorisations become influential in guiding the movement to a biased target location. Such effects are quite complex [25•], and they seem to involve differential involvement of the hemispheres [27]. Nevertheless, these phenomena are promising as paradigms for the study of brain mechanisms that underlie higher-order spatial aspects in motor control. Both functional-neuroimaging experiments in humans and neurophysiological recordings in monkeys can easily be used to investigate these phenomena.

Conclusions

The definition of the term 'cognitive' is becoming more and more blurred, as it is being used ever more frequently in diverse fields. Operationally, it can be taken to refer to covert processes in general. In that respect, this 'opinion' is focused on issues relating to covert processes at the base of motor control, namely spatial and temporal aspects. I have tried to delineate some of the complexities inherent in dealing with the elusive concept of space, and have brought to the foreground issues and concepts on temporal control, which were mainly developed in ecological psychology. Altogether, it seems that the methods used to extract spatial motor information from the neuronal populations share common formal characteristics with those functions that determine temporal courses: they can be widely and formally applied as computational algorithms for information processing. Finally, I have outlined new research directions that could yield novel information on neural mechanisms relating to the temporal control of movement. In turn, this new research on temporal control might provide fresh insight into the neural mechanisms underlying spatial motor control. At a higher level, the imitation of postures and moving from memory are very promising fields of investigation that may bring valuable new information to this always exciting and vexing subject.

Acknowledgements

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