J. Indian Inst. Sci.
A Multidisciplinary Reviews Journal
ISSN: 0970-4140 Coden-JIISAD

A Computational Framework for Understanding Eye–Hand Coordination

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Abstract | Although many studies have documented the robustness of eye–hand coordination, the computational mechanisms underlying such coordinated movements remain elusive. Here, we review the literature, highlighting the differences between mostly phenomenological studies, while emphasizing the need to develop a computational architecture which can explain eye–hand coordination across different tasks. We outline a recent computational approach which uses the accumulator model framework to elucidate the mechanisms involved in coordination of the two effectors. We suggest that, depending on the behavioral context, one of the two independent mechanisms can be flexibly used for the generation of eye and hand movements. When the context requires a tight coupling between the effectors, a common command is instantiated to drive both the effectors (common mode). Conversely, when the behavioral context demands flexibility, separate commands are sent to eye and hand effectors to initiate them flexibly (separate mode). We hypothesize that a higher order executive controller assesses behavioral context, allowing switching between the two modes. Such a computational architecture can provide a conceptual framework that can explain the observed heterogeneity in eye–hand coordination.

Keywords: *RT correlation, Accumulator models, Common command, Flexible coupling*

1 Introduction

Imagine walking into your kitchen to make a sandwich. Most of the movements that you will make therein require fine coordination between your eyes and hands. We execute such movements, since we are infants[1] to the very end of our lives, be it writing, reaching for an object and many other activities that are vital to our everyday lives.[2] Typically, while moving the hand to a particular location in space, a rapid eye movement, called a saccade is made which brings the region of interest into the fovea. Such a link between the two effectors might be a consequence of visual acuity being highest at the *fovea* in the retina and reducing towards the periphery. Making a saccade to the target provides accurate information regarding the target, and is crucial for the precise and accurate accomplishment of the hand movement. Thus, saccade onset usually precedes hand movement onset by $8^{0-1}00$ ms.[3,4] Nonetheless, we are also capable of generating eye and hand movements independent of each other when a behavioral context demands it. For example, saccades that scan the page while reading or the hand gestures that accompany conversation are scenarios in which eye and hand movements are executed in isolation. This indicates a functional independence between the two effector systems in certain behavioral contexts.

Although ethologically often coupled, eye and hand movements have been typically studied independent of each other. Studies in non-human primates have demonstrated that although both movements share common areas during early visual processing like V1 and V2, they diverge in the parietal cortex. While signals associated with saccades are observed in the lateral inter-parietal (LIP) area,[5–7] those related to hand movements

Fovea: Central part of the retina with maximum density of photoreceptors and hence the highest acuity.

Parietal Cortex: Part of the brain in between the anteriorly located frontal cortex and posteriorly located occipital cortex (involved in processing of vision). It is thought to play a major role in integrating sensory information from multiple sensory systems like vision, proprioception, touch, etc.

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Springer IISc Press

Frontal Cortex: Most anterior part of the brain, and thought to be involved in many functions like motor functions, language, memory, decision-making, social and sexual behavior, and many more.

Effectors: Organ or body part that can respond to the commands send from the central nervous system. In this manuscript, this term refers to eye and hand motor system.

Single neuron physiology: An invasive technique by which fine meta electrodes are inserted into the living brain of animals performing tasks. This allows us to record the neuronal responses in specific areas of the brain and correlate these responses to behavior.

Whole brain Imaging: A non-invasive technique that employs MRI and utilizes the differences in the level of oxygen in the blood to localize functions to specific regions in the brain.

End-point: The end-location of the movement, i.e. where the movement stops after initiating.

Amplitude: The absolute displacement of the movement.

RT correlation: Correlation between eye and hand RT.

Motor commands: The neuronal impulses send by the cortical areas to muscles so as to drive them. In this manuscript, the motor command results in rotation of the eye in the orbit or in the movement of the hand

RT: Time between the presentation of the target and the time of movement onset.

Perceptual input: The encoding of the visual targets in the brain.

Contralateral: The left side of the brain controls the right side of the body and vice-versa. Contralateral refers to that side of the body opposite to the area recorded or inactivated.

have been reported in the parietal reach region (PRR).[8–10] This dichotomy continues in the frontal cortex, with the frontal eye field (FEF)[11,12] and supplementary eye field (SEF),[13,14] being involved in the planning of the upcoming saccades, while the dorsal and ventral premotor cortices (PMd)[15–18] are involved in the planning of hand movements related to reach direction and grasp configuration, respectively. These regions also project to different target areas: FEF connects to superior colliculus (SC),[19,20] which, in turn, connects to the brain stem saccade generators,[21] which innervates the eye muscles. In contrast, the premotor cortex projects to the primary motor cortex,[22,23] which then connects to the spinal cord which has motor neurons that innervate the hand musculature. Thus, there are largely anatomically independent areas responsible for bringing about eye and hand movements. Based on these evidences, it is not unreasonable to assume that eye and hand effectors are functionally independent, since the neural circuits responsible for initiating these movements are anatomically distinct. Hence, this raises the simple but intriguing question as to how the eye and hand effectors are coordinated to generate visually guided hand movements when a behavioral task or context demands it. Research on eye–hand coordination has used multiple approaches to address the fundamental question of how the two effectors interact. Here, we suggest an approach, which, in accordance to David Marr's (1982) terminology, is to understand the computational problem, i.e., what is the purpose and logic of the computations that lead to eye–hand movements. We suggest that this computational approach may offer novel insights and mechanisms and also provide a linking hypothesis to bridge the conceptual issues as well as the empirical evidences across different scales and data sets, ranging from single neuron physiology to whole brain imaging and behavior.

2 Eye–Hand Coordination: Behavioral Studies

Eye–hand coordination is behaviorally studied in two domains: spatial and temporal. Spatial coupling is studied by testing how well the end-points, amplitude, direction, velocity, etc., of the ensuing eye and hand movements are correlated. Temporal coupling is studied by testing how well the initiation of the two movements is correlated, and whether the experimental manipulation of reaction time (RT) in one effector is reflected in the RT of the other effector. In this manuscript, we focus only on the temporal coupling of eye and hand movements.

2.1 Studies On RT Correlation

The extent of RT correlation observed between concurrently produced eye and hand movements varies between studies. Some studies have reported low RT correlation (0.1–0.4),[3,24–26] which suggests that the two movements are initiated by separate motor commands which share common perceptual inputs.[25–27] Other studies have noticed moderate (~ 0.6) to high (~ 0.9) correlation,[28–31] suggesting a common motor command initiating the two effectors.[32] Frens and Erkelens[30] hypothesised that this range of RT correlation might arise, because eye movements may be generated by two mechanisms: one driven by only visual information resulting in low RT correlations, and another 'more general purpose' mechanism used for the generation of eye and hand movements, which results in a higher RT correlation.

2.2 Studies On Change in RT

Some studies have reported that eye RT is modulated depending on whether it is accompanied by a hand movement or not,[4,31,33] suggesting a coupling between the eye and hand systems. Some studies have reported that both eye and hand RT are similarly affected by manipulations of the task design.[34–37] One such study by Fisk and Goodale[38] leveraged the anisotropy in the hand RTs when making hand movements to the ipsilateral and contralateral targets, where RT for the contralateral target is higher as the movement requires the hand to cross the midline of the body. However, the saccadic system, which does not show such RT anisotropy when executed alone, also exhibited similar anisotropic RTs when coordinated eye–hand movements were made, suggesting commonality in the programming of eye and hand movements. Another prominent example is the prevalence of a "gap" effect in the RT of concurrently produced eye–hand movements. The gap effect refers to decrease in RT when a temporal gap is introduced between the offset of the central fixation spot and the appearance of the peripheral target. However, when eye and hand movements are coordinated, the introduction of a gap affects both eye and hand movements to the same extent.[35] All these indicate that a common signal may be responsible for initiating the eye and hand movements. In contrast, Lawrence and Gardella [39] have demonstrated that eye and hand RT are affected differently depending on the number of distractors surrounding the target. While saccade RT decreased when the number of distractors increased, hand RT increased with increase in the number of distractors, indicating separate mechanisms of eye and hand initiations. In conclusion, based on these results, it is unclear whether common or interacting systems are responsible for the initiation of eye and hand movements.

3 Eye–Hand Coordination: Neurophysiological Studies

As mentioned before, the neuronal pathways responsible for initiating eye and hand movements have been typically thought to be anatomically distinct, but recent physiological recordings in awake behaving primates have shown that this distinction is not absolute. Studies have reported that the activity in areas like LIP, FEF, SEF, and SC that are classically considered to be saccade related is also modulated by hand movements. Thura and colleagues have found that the activity in the FEF, which was classically thought to be dedicated to saccade programming, could be modulated by hand position,[40,41] while Mushiake et al.[42] demonstrated that some SEF neurons preferentially activate in a saccade-reach condition compared to a saccade-only condition. LIP has also been implicated in integration of hand signals.[43] Similarly, the deep layers of SC show modulation of activity based on hand movements.[44,45] Conversely, areas which were classically considered to be hand-related such as PRR and the premotor cortex are also modulated by eye movements. For example, activity in the dorsal[46,47] and ventral premotor cortex[48] can be influenced by the position of the eye in the orbit and direction of gaze, respectively, while activity in PRR is also influenced by gaze direction.[49,50]

In addition to electrophysiological recordings, reversible chemical inactivation has been used to get a more causal and direct role of different brain areas in eye–hand coordination. Inactivation of monkey SC by *muscimol* not only affected saccades but also reach movements to the inactivated visual field.[51] This study showed that SC may be part of an effector-independent priority map from which a target may be selected for both eye and hand movements, thereby facilitating coordination. Similarly, inactivation of LIP has shown to affect coordinated eye–hand movements, but not hand movements that are executed in isolation.[52] However, similar inactivation experiments in the parietal area PRR that plays an important role in reaching movements have shown inconclusive results. For example, Yttri et al.[53] suggested that the inactivation of PRR had a main effect only on the contralateral reach RT, consistent with a limb specific representation in PRR, Christopoulos et al.[54] have reported that inactivating PRR affects the amplitude of both hand and eye movements if they are performed concurrently. In the former study, the RT correlation between the eye and hand was spared even after inactivation, while in the later study, the RT correlation decreases upon inactivation. Hence, the role of PRR in eye–hand coordination is not clear.

These neurophysiological evidences contradict the hypothesis of a complete anatomical independence between eye and hand effectors. Yet, these studies cannot clearly disambiguate if the modulation in the neural activity observed in these regions represents a common effector-independent representation or a consequence of effector-dependent representations that are interacting with each other. Moreover, since neurons in these regions were not classified as either visual or motor, it is not clear if these effector-specific modulations are responsible for spatial or temporal coordination observed in behavior. Hence, studies based purely on neurophysiological data cannot disambiguate these competing hypotheses.

4 Eye–Hand Coordination: Clinical Studies

In addition to the physiological studies done in monkeys, clinical studies have shown a specific neurological defect which involves the pathological yoking of eye and hand movements. For example, a patient who suffered from bilateral parietal lobe atrophy was unable to reach to targets that she was not allowed to foveate. When she attempted to reach for a target in extra-foveal vision, despite repeated attempts she inevitably reached to the fixation spot instead. This phenomenon characterised by a slavish dependence on eye position signals for guidance of the hand is called 'magnetic misreaching'.[55,56] Consistent with these reports, neuroimaging studies on normal human subjects have yielded evidence that parietal regions play a major role in eye–hand coordination. Some studies have observed an effector-independent common representation to be active in the parietal region when coordinated reach movements are planned.[55–59] In contrast, another study has shown that these areas are effector-dependent, conforming to the classical notion of independent anatomical pathways for

Reversible chemical inactivation: An invasive pharmacological method by which neuroactive substances are injected into specific regions in the brain, thereby creating temporary lesions. The altered behavior due to the lesion gives insight about the function of the lesioned region. The lesion is reversed once the neuroactive substance is washed away through normal metabolic processes.

eye and hand movements.[60] Hence, the results obtained from these studies are not conclusive and contradict each other.

5 Computational Mechanisms of Eye–Hand Coordination

The behavioral, neurophysiological, and clinical studies have presented numerous observations pertaining to eye–hand coordination, but barring a few, most have failed to provide a mechanistic basis for the observed results. As alluded to before, the previous studies have shown varying levels of RT correlations between eye and hand effectors, some demonstrating low correlations (0.1–0.4) and some high correlations (0.6–0.9). Though RT correlations have been used as a measure of coordination, their mechanistic interpretations remain unclear. The low correlations may have arisen due to the sharing of the lower perceptual inputs that drives both the effectors, while the studies that found a strong correlation indicate a common motor command initiating the two effectors. There have been no means to bring this wide variation in the observed data regarding eye–hand coordination with in the preview of a theoretical framework. In addition, how task manipulation affects eye and hand RT distributions also differ widely between studies. Hence, it is not clear what mechanism allows the effectors to behave in a coordinated or in an independent fashion. The wide variation of results observed in the literature suggests the possibility of three broad architectures underlying eye–hand coordination: the independent, interactive, and common command models.

EMG (Electromyography): Electrical signals denoting muscle activity recorded either using electrode placed on the surface of skin, or using invasive needle electrodes.

6 Independent Model

An independent model of eye–hand coordination assumes that eye and hand effectors are initiated by two separate networks that are completely independent of each other (Fig. 1a). The coordination is thought to be a passive process that may arise from the sharing of retinal inputs and perceptual processes that helps to encode the target. The functional independence of eye and hand effectors gives some credibility to this hypothesis. Moreover, studies that have shown independent allocation of attention for eye and hand movements[61] also lend support to this model. Behaviorally, studies that have also shown that certain illusions like the Titchener and Muller Lyer illusion which affects the saccadic system, but not the hand system [62,63] also endorse this model.

Titchener and Muller Lyer illusion: Optical illusion with line segments with arrow shafts at both ends of the line. The shafts of arrows can either point inward to form an arrow head, or point outward to form an arrow tail. The line segment enclosed by two arrow tails is perceived to be longer than the one enclosed by two arrow heads.

7 Interactive Model

An interactive model of eye–hand coordination suggests that coordination is an active process that is brought about through interaction between otherwise independent eye and hand networks (Fig. 1b). When movements are to be executed in isolation, the independent eye and hand circuits are separately engaged to plan the respective movements. This model can account for the functional independence of eye and hand movements. However, when a behavioral context demands coordinated movements, then these networks interact with each other, bringing about coordination that is reflected in the temporal correlations seen between eye and hand movements. In addition to these evidences, an interactive model may also beable to account for the range of RT correlations observed across the previously mentioned studies. To accomplish certain task, the effectors need to be tightly coupled, while, in some others, they may be loosely bound. An interactive model can take into account this dynamic range of eye–hand coordination by adjusting the strength of possibly interaction between the possibly independent networks.

8 Common Command Model

The common command model proposed to explain the coordination between two effectors-eye and neck,[32] has been adopted to explain the coordination between the eye and hand systems, as well.[64] This model suggests that coordinated eye and hand movements are initiated by a common command that descends from the cortex (Fig. 1c). Bizzi and colleagues observed that the electromyography (EMG) activation of the neck muscle happened prior to the saccade and was tightly linked to the saccade during a coordinated eye neck movement. Hence, they proposed that a single command initiates both the neck movement as well as the accompanying saccade. Similarly, Gribble et al.[65] observed that the EMG activation of the shoulder occurred around the time of onset of saccades, even though the hand initiation was much later than the initiation of the eye movement. Studies that have reported a concomitant change in one effector when the other effector changed also support this model. However, by far, the strongest proof of this model stem from the reports of a strong temporal correlation between eye and hand RT. Furthermore, results that show that task modulation that lead to the similar modulation in eye and hand RT also ratify this model.[4,33] However, numerous studies have also reported low-to-moderate correlations, which argue against the common command model, as this model does not provide flexibility. Hence, a common command model may be considered as a dedicated network that is exclusively used to generate coordinated movements.

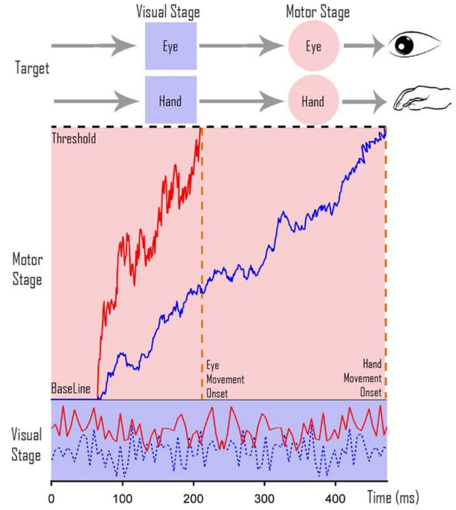
9 Computational Approaches to Understand Eye–Hand Coordination

Despite numerous studies on eye–hand coordination which draw on different approaches such as psychophysics, neurophysiology, and neuroimaging, there is no clear consensus regarding the architecture that generates coordinated eye–hand movements. There has been a little effort so far to understand the wide variation in the data observed and to conceptualize a computational architecture that can explain the data. Recently, Dean et al.[26] have tried to bridge this lacuna using the computational framework afforded by accumulator models of decision-making and RT to study the mechanisms underlying eye–hand coordination. The accumulator framework is based on the fact that in real world, sensory signals are noisy due to the noise present in the sensory transduction pathways as well as inherent stochasticity of neurons. If decisions are made based on random sampling of such noisy signals, then decision can often be erroneous. Hence, cumulative summing of the signal across time may be a more appropriate strategy for making decisions. Consequently, when the noise in the sensory signal is greater, a longer sampling time is required to generate accurate decisions. This cumulative summing is embodied in this theoretical framework as an accumulator that accumulates sensory evidence in favor or against a decision to a threshold. When the threshold is crossed, the decision is made and the time the accumulator took to reach the decision threshold contributes to the decision time which is the major component of RT. This model can also be used in the case of a simple detection task where a subject detects a target and then respond to it by a movement. The motor plan or the series of mental processes that are involved in transforming a visual target to the intended movement can be abstracted to an accumulator that accumulates information to a threshold. When the accumulator reaches the threshold, a movement is thought to be initiated. The noise in the sensory signal as well as in the neuronal networks is reflected in the accumulation process resulting in trajectories of the accumulator which vary from trial to trial, leading to a distribution of threshold crossing times across trials. Thus, this model is able to account for the variability in the RT distributions seen in the data.[64–71]

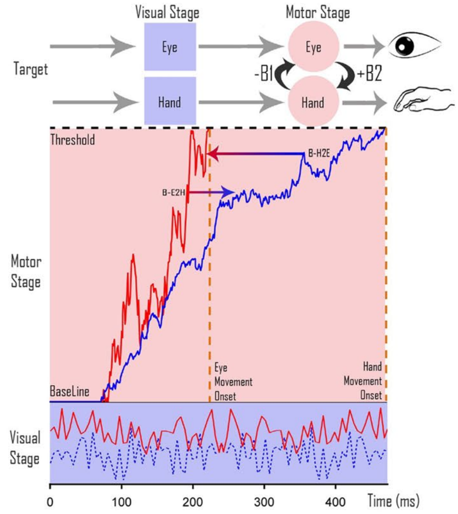
Dean et al.[26] used this accumulator framework to understand the data recorded, while the monkeys performed a dual task, where the eyes had to be directed to a peripherally appearing target, while the hand had to be moved to the same target if an auditory tone was also presented. They systematically varied the time between the presentation of the visual target and the auditory tone (called the Stimulus Onset Asynchrony or SOA) and measured the eye and hand RT, and the correlation between the RT of the two effectors. Although results were inconsistent between monkeys, behaviorally, they observed low RT correlation across SOAs. Furthermore, eye RT tended to increase, while hand RT tended to increase and then decrease as a function of SOA. They tested different accumulate to threshold models; where the eye and the hand systems had their individual accumulators and were driven by a common noise signal; common neuromodulation; shared signals; or by mutual excitation with individual sensory signals. The model with accumulators having unequal mutual excitation was best at explaining the RT correlation across SOA, and the general pattern of RT across SOA.

This approach was extended by Gopal et al.[31] in which normal human subjects performed a simple pointing/reaching task to a target that appeared peripherally on either side of a central fixation spot. Subjects performed this task under three different conditions; eye-alone when the hand remained at the centre, while the subject looked at the peripheral target; hand-alone when the subject remained fixated at the centre and point to the peripheral target; eye–hand when the subject looked and pointed at the peripheral target. They hypothesised that some behavioral indications of coordination could be seen by comparing the responses of eye and hand when executed in isolation to the condition when the same effectors were coordinated. Consistent with some of the previous results, in the coordinated eye–hand condition, the eye RTs were faster compared to the hand RTs and there was a strong trial-by-trial correlation between the RTs of eye and hand. To understand how coordinated eye–hand movements are planned, the three architectures of eye–hand coordination were modelled using an accumulator framework, which predicted RT distributions of eye and hand effectors and their correlations. The independent model did not capture the high RT correlations seen in the data. Hence, they concluded that eye–hand coordination is an active mechanism and the

(A) ***Independent Model***



(B) ***Interactive Model***



(C) ***Common Command Model***

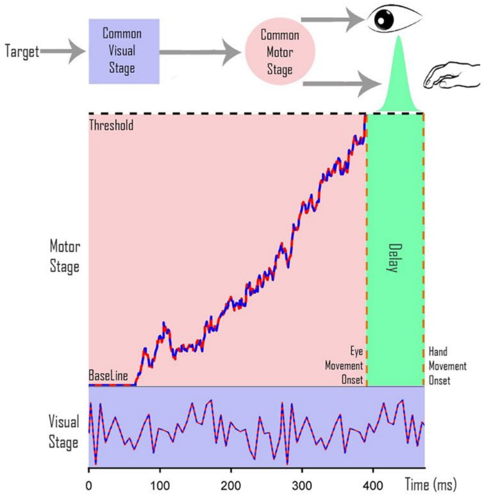


Figure 1: Architectures of eye–hand coordination: Schematic of the three potential architectures of eye–hand coordination is shown (adapted from Gopal et al.[31]). A possible architecture is schematized with separate visual stage (purple squares) where the targets are encoded, and a motor planning stage (pink circles). Bold red (eye) and the dashed blue (hand) trace represents separate stochastic sensory signals which are integrated over time to reach a threshold indicated by the dashed black line. Each movement is executed as soon as the respective accumulator reaches threshold. **a** Independent model in which eye and hand effectors have completely distinct and separate visual and motor planning stages, but are passively coordinated by the common target. **b** Interactive model comprising of independent eye and hand networks that interact (black arrows) at the level of motor planning. **c** Common command model with a common visual and a common motor planning stage. Dashed red–blue trace represents the common stochastic sensory signal that is integrated over time to reach the threshold. Saccades are executed when the common signal reaches the threshold, while the hand movement is executed after a temporal delay with Gaussian jitter (green).

passive independent model was not capable of generating coordinated movements.

In their data set, that mean eye RTs in the eye–hand condition were slower by ~ 50 ms compared to the eye-alone condition, while the mean RTs of the hand in the eye–hand condition were faster by ~ 100 ms compared to the hand-alone conditions. This shifting of the RT distributions was inferred to reflect an active mechanism that generates coordinated movements and was modelled as an interaction between the eye and hand effector systems. An inhibitory interaction from the hand accumulator to the eye accumulator diminished the rate of accumulation of the eye, resulting in slower saccade onset, while an excitatory interaction from the eye to the hand accumulator enhanced the rate of accumulation of the hand, resulting in a faster hand movement. While this model could explain the shift in the means of eye and hand RT seen across conditions, it could not predict the standard deviations (SDs) of the hand RT distributions. Moreover, this model also failed to generate strong RT correlations that were observed in the data.

The authors observed that the SDs of eye and hand RT distributions in the eye–hand condition were comparable, even though the mean of the distributions was different by 100 ms (Fig. 2a). This result was quite intriguing, since previous experimental studies have shown earlier that the SD of RT distribution scales with its mean. In the theoretical framework of accumulator models, trials with a longer RT are a resultant of longer accumulation, during which noise also accumulates, resulting in greater variability in the RT distributions. Hence, the SD of the RT distribution is thought to increase linearly when the mean of the distribution increases.[72,73] This observation which contradicts the accumulator model proved to be the most crucial evidence for the common command model of eye–hand coordination, which hypothesises that the eye and hand effectors in the eye–hand condition are initiated by a common accumulator that rises to a common unitary threshold. Since the amount of noise accumulated in the stochastic accumulator manifests as the SD of the RT distribution, a common accumulator that initiates eye and hand movements will result in a comparable SDs for both the distributions. The difference in the eye and hand RTs was taken into account by incorporating a delay between the time the common accumulator reaches the threshold and the actual initiation of the hand movement, a delay which relates to the delay in activation of the hand muscles to initiate the movement. The common command architecture could account for the means, the SDs, and the correlations of the eye and hand RT distributions. They physiologically validated the common command architecture by recording EMG from the shoulder muscle of the pointing arm of subjects performing coordinated eye–hand trials. Not only did the EMG onset occur ~ 50 ms prior to the onset of the saccades, there was also a strong correlation between EMG onset and saccade onset, which strongly suggested that EMG onsets represent the termination of the common accumulation at the unitary threshold after which a common command is sent downstream to the effectors to initiate the eye and hand in the coordinated condition. More importantly, the delay measured from the EMG (time interval between hand onset and EMG onset) and the delay predicted from the common command model were well correlated. However, a common accumulator which controls the initiation of both eye and hand effectors is expected to produce a perfect correlation, which is never observed in the data. To account for this, the hand delay was modelled as a stochastic variable to include trial-to-trial variability which was termed as motor noise, which de-correlated the perfectly correlated RTs that was generated by the common accumulator. Taken together, their results suggest

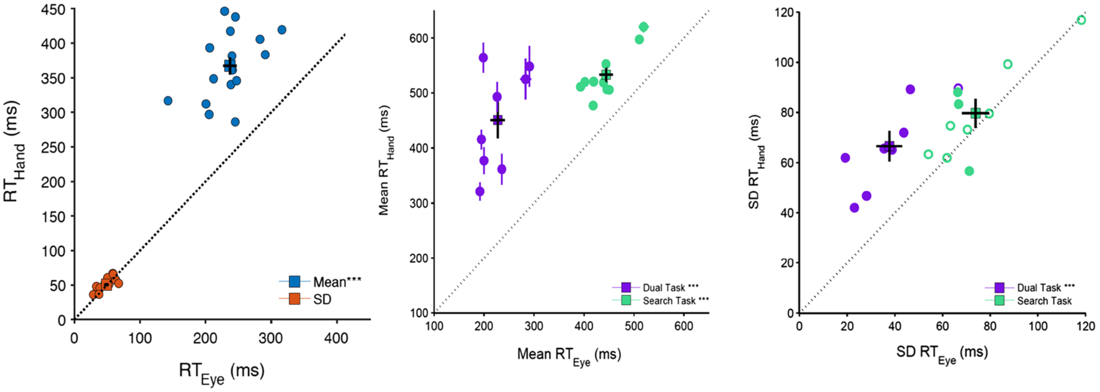


Figure 2: Mean–SD relationship for RT distributions (**a**) Comparison of the means (blue dots) and SDs (red dots) of eye and hand RT distributions, where each dot represents a subject, while the square and black cross-hairs represent the population mean ± SEM. The black dotted line represents the unity line. While the mean hand RT is significantly greater than the mean eye RT, the SDs of the eye and hand RT distributions are comparable (adapted from Gopal et al.[31]). **b** Scatter plot comparing the mean eye and hand RT in the Dual task (purple dots) and Search task (green dots). Conventions are same as in **a**. In both the Dual task and Search tasks, the mean hand RT is significantly greater than the mean eye RT (adapted from Jana et al.[74]). **c** Comparison of the SD of eye and hand RT distributions in the Dual task (purple dots) and Search task (green dots). The unfilled dots represent subjects where the SD of eye and hand RT distributions are comparable. Other marking conventions are the same as in (**a**). The SD of the eye and hand RT distributions are comparable in the Search task, but in the Dual task, the SD of hand RT distribution is significantly greater than the SD of eye RT distribution (adapted from Jana et al.[74]).

that the common command is a physiologically valid architecture that brings about coordination between eye and hand effectors.

10 Flexibility in Eye–Hand Coordination

While the common command architecture is able to explain high RT correlations, it may be unable to explain the data of studies which have shown low RT correlation. Thus, it seems that eye and hand systems are flexibly coupled and that the task context determines the coupling between the two effectors. Highlighting this, Sailer et al.[25] tested participants on various eye–hand tasks and observed varied level of correlation between eye and hand RT. Motivated by these issues, Jana et al.[74] tested human participants in two contrasting behavioral contexts, one in which the two effectors were expected to be coupled, and another context where they were expected to be decoupled, and tried to elucidate the computational architecture underlying the flexible coupling of eye–hand movements. One context was a search task where subjects had to make an eye–hand movement to the odd colored target embedded among similar colored distractors, where the effectors were expected to be coupled. The other context was a dual task (similar to the one used by Dean et al.[26]), where the eye movement was to be directed to a peripherally appearing target and the hand movement was to be initiated only if a tone was presented; in this context, the two effectors were expected to be decoupled. Although hand RT was significantly greater than eye RT in both task contexts (Fig. 2b), interesting differences were observed in terms of RT correlations and the SD of eye and hand RT distributions. In the Search task, RT correlation was high and the SDs of eye and hand RT distributions were similar, while in the Dual task RT, correlation was low, and SD of hand RT was significantly greater than the SD of eye RT distribution (Fig. 2c). Similarly, while saccade and EMG onsets were strongly correlated in the Search task, they were weakly correlated in the Dual task. While both the common command and interactive models could predict the mean RT, only one could predict the SD of the RT distributions and RT correlation. In the Search task, the common command model could predict the SD of RT distributions and the RT correlation, but the interactive model could not. In contrast, the data in the Dual task were best explained by the interactive model, but not by the common command model. Interestingly, they also observed a small subset of trials in the Search task where the behavior followed the prediction of the interactive model, i.e., low RT correlation and non-comparable SDs of eye and hand RT

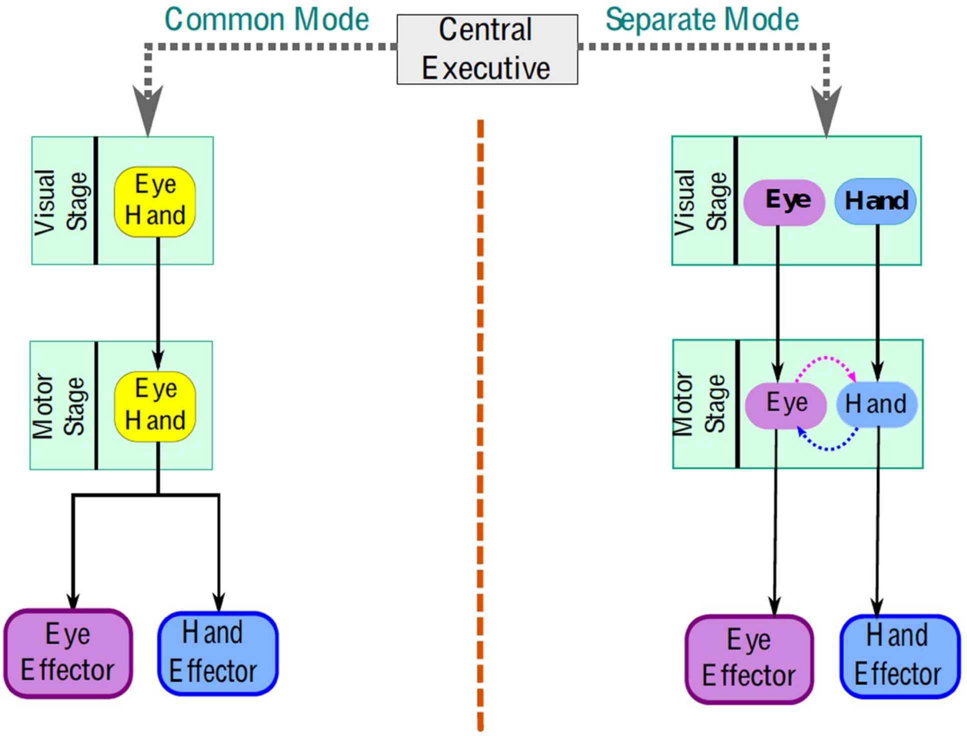


Figure 3: Putative computational architecture underlying eye–hand coordination. We hypothesize that there are two modes of generation of eye–hand movements, a default mode which has common planning stages for the eye and hand systems, and a non-default mode which has separate planning stages for the eye and hand systems. For each movement, there are two main planning stages, a visual stage, where the retinal target information is encoded in the brain, and the appropriate target is selected, and a motor stage, where the time of movement onset is computed. For the common mode, the visual and motor stages are common for both eye and hand system, i.e., a common network is used to process these two decisions for the two effectors. For the separate mode, the networks processing the decisions for the two effectors are separate with interaction between the two networks. In addition, we propose that there may be a higher order area which acts like a central executive controller, which depending on the task demands, chooses which mode to use for generating eye and hand movements.

distributions. This suggested that the task context merely biases the brain towards one or the other architecture, indicating that higher executive control structures may participate in switching from a common accumulator to an interactive accumulator architecture.

11 Conclusion

Most eye–hand studies have in essence suggested an architecture where the accumulators for the eye and hand are either common or separate. Such a dichotomy may be artificial. In light of the heterogeneity of results seen across tasks, and based on the results of Jana et al.[74], the architecture underlying eye–hand movements should be extended to include both modes of operation (Fig. 3). It is conceivable that there are two modes of generation of eye–hand movements, one mode where there is a common visual and a common movement stage for these effectors. This might indicate a dedicated network for executing eye–hand movements in task contexts which require fine temporal coupling between the two effectors, like reaching for a glass of water. A large repertoire of eye–hand movements that we generate in our daily lives might use this circuitry. However, this mode is inflexible as it will not be able to generate movements where there is a requirement to decouple eye and hand movements. Another mode of operation may be where each effector has its own visual and movement stages, with some interaction between the two effectors. This might indicate two separate networks being used for the initiation of the two effectors, and might be used in a specific context where there is a need to decouple the eye and hand movements,

Central executive: A higher brain center that controls and supervises the functions of other lower areas.

like playing drums. Thus, there may be a central executive process that, depending on the task demands (and level of expertise), selects the mode of initiation of eye–hand movements. This selection may be trial-by-trial or may be spanning multiple trials, reflecting a kind of motor set. However, such a selection may not absolute, i.e., there may be occasional trials where instead of using the default mode for that task context, the non-default mode is used instead. This highlights the tremendous flexibility and in effect suggests a computational architecture that can encapsulate large cohorts of behavioral data observed across studies.

Received: 22 September 2017 Accepted: 24 October 2017

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