Université de Montréal

An investigation of reach decisions during ongoing action control

Par

Julien Michalski

Département des neurosciences, Faculté de médecine

Mémoire présentée à la Faculté de médecine en vue de l’obtention du grade de
maîtrise en Neurosciences

Août 2020

Université de Montréal

Département des neurosciences, Faculté de médecine

Ce mémoire intitulé

An investigation of reach decisions during ongoing action control

Présenté par

Julien Michalski

A été évalué par un jury composé des personnes suivantes

Trevor Drew

Président-rapporteur

Paul Cisek

Directeur de recherche

Andrea Green

Codirecteur

Aarlenne Khan

Membre du jury

ABSTRACT (Français)

Les études neurophysiologiques de la prise de décision, traditionnellement ancrées dans des principes neuro-économiques, ont évoluées pour inclure une variété d'aires du cerveau. Partant d'abord du lobe frontal associé aux jugements de valeur, le champ s'est élargi pour inclure d'autres types de décisions incluant les décisions perceptuelles et les décisions incarnées qui impliquent notamment les aires sensorimotrices du cerveau. La théorie moderne de la prise de décision modèle l'activité neurale dans ces régions comme une compétition entre les différents stimuli et actions considérés par un individu. Cette compétition est résolue lorsque l'activité neurale associée à un stimulus ou une action choisie atteint un seuil critique. Toutefois, il reste à éclaircir comment ce modèle s'applique aux décisions effectuées alors que l'individu est déjà engagé dans une activité. Dans ce mémoire nous examinons ce type de décision chez des sujets humains dans une tâche de suivi continu. Des cibles « choix » apparaissaient sur un écran pendant que le sujet suivait de la main une cible qui se déplaçait doucement en continu. Le sujet pouvait ignorer ces cibles choix, ou abandonner la cible suivie pour toucher une cible choix, dans quel cas la cible sélectionnée devenait la nouvelle cible à suivre du doigt. Tel qu'attendu, nous avons observé que les sujets favorisaient les cibles plus proches, plus grandes, et les cibles alignées avec l'axe du mouvement. Toutefois nous avons été surpris de constater que les sujets ignoraient les coûts énergétiques du mouvement, tel que modélisés. Un biais pour minimiser les coûts du mouvement fut réintroduis lorsque la tâche fut divisée en séries de mouvements point-à-point, plutôt qu'un mouvement continu. Même si nous ne pouvons expliquer ce résultat surprenant, nous espérons qu'il inspire de futures études utilisant le paradigme expérimental de décision durant l'action.

Mots clés : Biomécanique, contrôle moteur, décision perceptuelle, décision incarnée, modèle de diffusion, modèle neuro-économique, mouvement d'atteinte, prise de décision

ABSTRACT (English)

Neurophysiological studies of decision-making have expanded over decades to involve many brain areas. The field broadened from neuroeconomics, mainly concerned with frontal regions, to perceptual or embodied decision-making involving several sensorimotor areas where neural activity is linked to the stimuli and actions necessary for the decision process. Current models of decision-making envision this neural activity as a competition between different actions that is resolved when enough activity favors one over the other. However, it is unclear how such models can explain decisions often present in natural behavior, where deliberation takes place while already engaged in an action. In this thesis, we examined the choices human subjects made as they were engaged in a continuous tracking task. While they were manually tracking a target on a flat screen, subjects were occasionally presented with a new target to which they could freely choose to switch, whereupon it became the new tracked target. As expected, we found that subjects were more likely to move to closer targets, bigger targets, or targets that were aligned to the direction of movement. However, we were surprised that subjects did not choose targets that minimized energetic cost, as calculated by a biomechanical model of the arm. A biomechanical bias was restored when the continuous movement was broken up into a series of point to point movements. While we cannot yet explain these findings with certainty, we hope they will inspire further studies using decide-while-acting paradigms.

Key words: Affordance competition hypothesis, Biomechanics, Decision-making, Drift-diffusion model, Embodied decision, Motor control, Neuroeconomics, Perceptual decision, Reaching

TABLE OF CONTENTS

TABLE OF FIGURES:

LIST OF ABBREVIATED TERMS:

ACC – Anterior cingulate cortex

AUC – Area under the curve

dlPFC – Dorsolateral pre-frontal cortex

DV – Decision variable

FEF – Frontal eye fields

fMRI – Functional magnetic resonance imaging

GVS – Galvanic Vestibular Stimulation

LIP – Lateral intraparietal area

M1 – Primary motor cortex

MEP – Motor-evoked potential

MT – Middle temporal area

nAC – Nucleus accumbens

OFC – Orbito-frontal cortex

PPC – Posterior parietal cortex

RT – Reaction time

S1 – Primary somatosensory cortex

S2 – Secondary somatosensory cortex

SRT – Switch reaction time

TMS – Transcranial magnetic stimulation

vmPFC – Ventromedial pre-frontal cortex

1.0 Chapter 1: Introduction

In our daily lives, we are confronted by a multitude of choices. While many decisions are abstract or occur at defined moments, such as choosing a career, other decisions are more concrete and reactive, such as navigating the traffic during a daily commute. These types of decisions require the brain to generate the movements (such as steering to turn right) necessary to achieve a goal or destination while constantly being ready to change the current motor plan to react to a change in stimuli (like a previously unseen cyclist overtaking you). While there are many studies investigating how we move and many of how we choose, few studies look at how we choose while moving. Depending on how far you are in the turn and how fast you are going, you might need to step on the brakes and/or steer left more or less abruptly. Since the implementation of such "embodied" decisions is dependent on the movement you are currently engaged in, it seems likely that the current motor plan that must be overwritten has an impact on the decision about how to react next. For this reason, studying decision making while subjects are already engaged in a task might reveal new information on the decision process.

Our initial understanding of decision-making came from studying how people value different options offered to them. This concept of value allows the brain to reduce different options to a common currency where a comparison can be made. However, this economic concept is concerned with a relatively limited type of decisions and promoted an understanding of decision-making as a sequential process: first evidence is gathered by the senses, second a comparison is made during deliberation and third, an action is performed as the outcome of the decision. As decision-making research expanded its reach into the brain, it became apparent that the decision process couldn't easily be segregated into a sequence. Instead, perceptual decision-making experiments showed how the senses participate in deciding, and embodied decision-making experiments revealed that the potential outcomes of decisions also influence how we choose. Here, I will first discuss these theories of decision-making and present a few examples studies that illustrate key findings to demonstrate that decision-making is a continuous process involving several areas of the brain, each playing a role in making a choice I will also raise some questions as to how those theories might apply to decisions made during ongoing action and highlight the need for studies that involve those types of decisions. In the discussion chapter, I review our motivation for the study presented in the joined paper, as well as our results, before commenting on limitations, suggesting avenues for improvement and future studies that the decide-while-acting experimental paradigm could offer insights with the ultimate goal of improving our models of decision-making.

1.1 Economic decisions

1.1.1 General description

Economic choices are typically conceptualized as the process of choosing the option that awards the best subjective value or outcome (Padoa-Schioppa and Assad 2006). Neuropsychological studies of decision-making have traditionally focused on classic economic decisions where choices and their outcomes are represented as values weighed against each other to select a preferred outcome.

Many factors can influence the perceived value of an option in relation to another. Buying a house for example will have many determinants, like size, cost, distance from work, etc. that can influence its desirability. By integrating the different determinants into a single value for each option, the chooser has a common scale to weigh substantially different choices against each other. In other words, by assigning value to options, we can compare apples to oranges when picking a snack that reflects both subjective and objective qualities of the choice.

1.1.2 Neural correlates of value

To investigate where this process of assigning value might occur, scientists sought neural correlates of value by recording neurons in specific areas of the brain showing increased activity during an economic decision. An example of a typical task design of economic choice in monkey would have the monkey choosing between receiving a quantity of juice A vs a quantity of Juice B. By varying the amount of each juice offered in each trial, it is possible to examine the relative value to the monkey of the two goods being offered (Padoa-Schioppa and Assad 2006). During this task, the researchers recorded in the orbitofrontal cortex (OFC) and found a first class of neurons whose activity linearly correlated with the quantity of one of the juices offered, a second class of neurons that fired according to the ratio of the chosen versus unchosen juice, and a third class of neurons that fired in a binary fashion, responding only to a single juice type.

The second class of neurons observed there, often referred to as “chosen value” neurons, are particularly interesting because they correlate with the behavior of the test subject and can be a direct observation of a measure of subjective equivalence between two different goods. When their spike rate is plotted against the ratio between the 2 choices, the peak of the U-shaped curve coincides with the point of relative equivalence between juice A and B. In other words, the firing rate was highest when the ratio clearly favored one option over the other, which the monkey would end up picking. However, the firing is at the lowest when the subject is just as likely to pick one option over the other (choosing x amount of juice A over y amount of juice B in 50% of the trials). This spiking behavior reveals a comparison between juice types and quantity that reveals both the preference of the monkey, and its ambivalence when the offers are equivalent.

The first class of neuron also strongly supports a neural representation of value as their firing rate is highest when the preferred juice is in a favorable ratio but is at its lowest when the ratio reaches the point of subjective equivalence. In essence, this neural activity reflects the quantity of juice but is scaled relative to the point of subjective equivalence for that particular trial. The authors also demonstrated that the spiking patterns are divorced from the visuo-motor contingencies of the task; the arrangements of the choice display or the eye movement required to pick a juice did not influence the neural activity of the recorded OFC neurons. This serves as direct evidence that the brain can make choices based directly on the estimated value of the goods offered.

In humans, typical studies often involve giving subjects a budget that they can use to bid on desired items. In a study by Plassman et al.(Plassmann, O'Doherty et al. 2007) subjects that had not eaten for 4 hours would go through a series of trials on which they bid on one of 50 familiar food items while sitting in an fMRI machine. At the end of the experiment, one trial is chosen at random and the subject receives the food item in exchange for the bid he or she made, while also keeping any leftover money from their budget. This ensures that every trial matters to the same extent for the subject.

Two types of trials were offered: free trials where the subject could choose what they were willing to pay to obtain the presented food item, or forced trials where the food items were presented with a price and the subject could accept or refuse the deal. The forced trials are important because the subject does not have to determine what he or she is willing to pay. This allows identification of the brain regions specifically involved in the choice of what to bid. Specifically, a brain region that is more active in free trials but not in forced trials for the same food item can be assumed to be involved in determining what the subjects is willing to pay, rather than in some other activity that the brain performs (such as simulating the taste of the presented food).

Researchers sought areas where the BOLD fMRI signals showed both an increased activity that correlates with willingness to pay during free trials and that were significantly more activated during free trials than during forced trials. The medial OFC and the dlPFC both satisfied those conditions, confirming the results from primate studies that these areas are involved in estimating the value of a choice.

Other neurophysiological experiments in primates (Kable and Glimcher 2007, Plassmann, O'Doherty et al. 2007, Kim, Hwang et al. 2008) and imaging studies in humans (De Martino, Kumaran et al. 2009, FitzGerald, Seymour et al. 2009) have also demonstrated neural correlates of economic value in the OFC and also in the ventromedial prefrontal cortex (vmPFC).

1.1.3 Neural correlates of the determinants that make up value

While value can serve as a common currency to compare options, researchers have also sought to identify what informs this value, and have broken it into several determinants of choice such as risk, by offering choices with probabilistic rewards (Peters and Buchel 2009), or temporal discounting by offering delayed rewards (Gregorios-Pippas, Tobler et al. 2009). Further evidence for the role of the vmPFC and OFC can be found in lesion studies examining how the construction of value is perturbed by damage to those areas. (Noonan, Walton et al. 2010).

More recent studies of economic choice have also examined the role of the striatum, particularly the nucleus accumbens (nAC) whose neuronal activity is strongest when choices are ambiguous or risky (Floresco 2015). However, the nAC's involvement seems to be geared more toward action selection or outcome rather than value calculation (Burton, Nakamura et al. 2015).

This points to some of the unresolved questions surrounding theories of economic choice which typically frame decision-making as a sequential process: first the relevant evidence is gathered by the senses, then deliberation takes place as values are compared and finally a choice is made and an action plan is formulated and expressed as behavior. But where is the line drawn between the processes of decision-making and action selection, especially when brain regions involved in sensorimotor transformations such as the lateral intraparietal cortex (LIP) can be shown to encode the values of actions and the decision between them (Platt and Glimcher 1999)? There are many decision scenarios where the actions resulting from a decision are relevant to the decision process, and where economical decision making isn't sufficient to generate an appropriate behavior. What if the options encountered are not discrete, there is not enough information establish action value, or conflicting choices are encountered sequentially? In such scenarios, decisions are seemingly illogical or inconsistent with models of economic behavior.

A commonly cited example of inconsistent economic behavior is the case when transitivity of preference is violated. Transitivity of preference holds that if choice A is preferred over B, and B is preferred over C, then A should also be preferred over C. However, transitivity violation can sometimes be observed (Tversky 1969, Shafir, Waite et al. 2002). In one particular study, subjects had to choose between pairs of gambles. Researchers observed clear systematic intransitive choices in many instances. In one case, a participant selected gamble A over gamble B in 100% of AB presentations, and chose gamble B over C in 80% of BC presentations, but chose A in only 5% of AC presentations even though A should be strongly preferred over C according to transitivity (Kalenscher, Tobler et al. 2010). Further investigation of the subject's behavior show that they changed their preference for safer or more rewarding gambles depending on the pair of gambles offered, suggesting that computations of value are context dependent.

Neuroeconomic studies laid a strong foundation for our understanding of decision-making by providing evidence that the brain constructs a common currency used in a comparison between choices. However, their limitations motivated scientists to look into other areas of the brain and other types of decisions to get a more comprehensive picture of decision-making.

1.2 Perceptual decisions

1.2.1 General Description

In recent decades, another type of decision has progressively gained more attention from neuroscientists: perceptual decision making (Shadlen, Britten et al. 1996, Smith and Ratcliff 2004). Instead of choosing which car to buy or what to eat, perceptual decisions focus on how the environment informs our behavior like stopping at a red light or determining if a food is still good to eat based on its color and odor. This type of simple decision involves matching a perceptual input (stimulus) with knowledge stored in memory to decide how to react to the stimulus.

This approach to decision making encouraged scientists to rethink the various elements that go into such decisions. First there are the priors: knowledge derived from previous experience which can inform the subject on possible outcomes. Second is the evidence, the stimulus used to inform the current decision. Third is the value which, as in neuroeconomics theory, is a measure of expected usefulness of the outcome. These 3 discrete elements combined can be thought to represent a decision variable (DV). This decision variable is not discrete, but rather a combination of everything that motivates a decision into a variable quantity which can be used as the common scale needed to compare apple to oranges.

Finally, the decision variable is interpreted according to a decision rule. The rule lets the subject decide how and when to interpret the decision variable essentially capturing the context surrounding a decision. The application of this rule is necessarily directed towards goals because even if prior knowledge and previous experience allows one to know that the walk signal is a good time to cross the street, this decision really only needs to be considered if one wishes to cross. In other words, the decision rule can be thought to govern the commitment to a decision.

1.2.2 Neural correlates of DV

Evidence of the decision variable can be found in several places in the brain (Gold and Shadlen 2007). Since these decisions involve extracting pertinent information from sensory inputs, researchers have looked into sensory regions related to different modalities to see how this information is represented. A few examples of studies where neural activity is correlated with the DV are described below.

1.2.3 Vibrotactile frequency discrimination task

In vibrotactile frequency discrimination tasks monkeys must decide which of 2 vibrations has the higher frequency. In the primary somatosensory cortex (S1), the neural firing rate increases with the frequency, but quickly returns to baseline when the stimulus disappears (Hernandez, Zainos et al. 2000). This region reflects a simple representation of a stimulus. However, in some brain regions downstream of S1 like the secondary somatosensory cortex (S2) the dorsolateral prefrontal cortex (dlPFC) and medial and ventral premotor cortices, the firing rate doesn't return to baseline during the delay between a pair of vibrations. Instead it stays elevated until the second stimulus is presented, at which point the firing rate increases or decreases depending on whether the frequency of that second stimulus was higher or lower. Although the neural activity during the delay could be a trace memory of the first stimulation preserved until a comparison is possible, this can also be thought of as a DV because it is updated with the second stimulus to reflect a prediction of the decision.

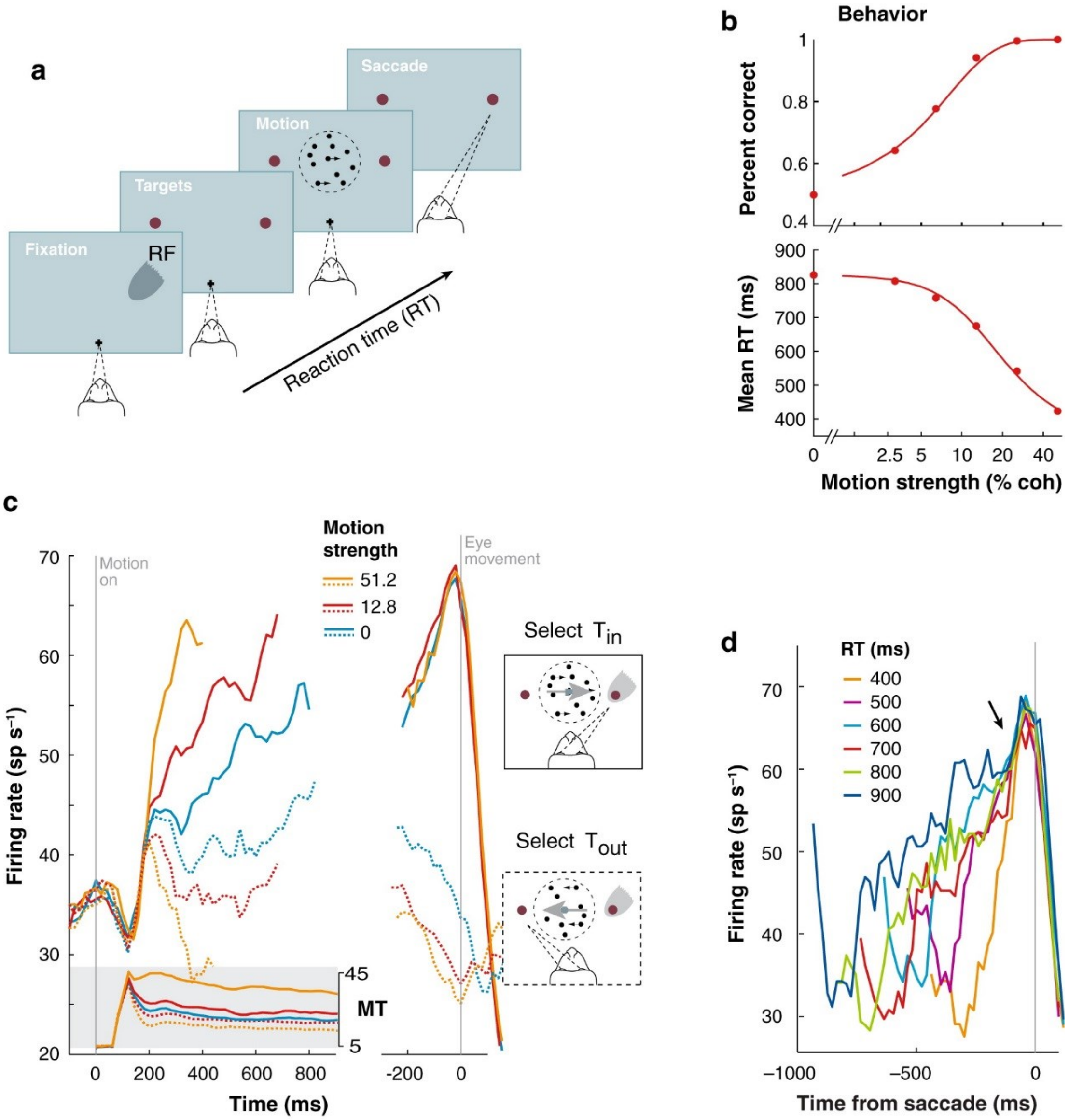
1.2.4 Visual Search task

In visual search tasks, subjects must pick out a target from among distractors. Such experiments were also foundational to this field, offering neural correlates between visual stimuli and gaze shifts. For instance, recordings in the frontal eye field of monkeys (Thompson, Hanes et al. 1996) show that neurons initially do not discriminate between the response target and distractors. However, the pattern of activity quickly separates and starts to discriminate targets, showing increased activity towards the response target while activity associated with a distractor target is suppressed. Interestingly, the discrimination occurs even if the gaze shift isn't produced, implying that the DV that favors the selection of the response target is encoded in the neuron's activity even in the absence of behavior. In this experiment the activity in a sensorimotor region such as the FEF might be enough to explain the choice behavior.

1.2.5 Random dot motion discrimination task

Another cornerstone experiment of perceptual decision making uses a field of randomly moving dots as a noisy stimulus, while the subject is tasked to indicate the net direction of motion of a subset of the dots that move coherently (Roitman and Shadlen 2002) (Figure 1.1a). By varying the coherence (proportion of dots moving in a net direction), scientists can control the amount of noise and thus the ambiguity of the motion stimulus. This is reflected in the neural activity of the medial temporal visual area, an area sensitive to visual motion (Britten, Newsome et al. 1996). A brief electrical microstimulation of the FEF during the task can shift the subject's gaze in the direction of the perceived net dot motion(Gold and Shadlen 2000). This gaze shift is dependent on the coherence and viewing time, suggesting that neurons in this region are either taking part in, or at least "informed" of the deliberation occurring in real time. In other words, these evoked gaze shifts seem to reflect the evolution of the DV as it is being computed in a sensorimotor area.

This neural pattern is seen in many gaze control areas such as the lateral intraparietal cortex (LIP) (Roitman and Shadlen 2002), the FEF (Gold and Shadlen 2000) and superior colliculus (Horwitz and Newsome 1999) (Horwitz and Newsome 2001) where neural activity reflects the accumulation of perceptual evidence as much as it predicts the choice that will be made (Figure 1.1c). This is also apparent in error trials, when the noise in the sensory system favors increased activity in the wrong direction (i.e., opposite to the net motion), causing the subject to choose the wrong target. Here again, sensorimotor regions seem to be involved in the decision directly based on the evidence.



Gold JI, Shadlen MN. 2007.
Annu. Rev. Neurosci. 30:535–74

Figure 1.1: Behavior and neural recordings during the random-dot motion task. A: Schematic illustrating the choice-reaction time version of the random dot motion task. The subject observes a patch of dynamic random dots and tries to determine the net direction of the motion (right or left) by redirecting his gaze to a peripheral target (red). The RF patch shows the response field of an LIP neuron. B: Effect of the difficulty (motion strength) on the accuracy and response times. C: Left: Firing rates of LIP neurons during deliberation. An average of 54 neurons is shown for three levels of difficulty motion strength), with the responses aligned to the onset of random-dot motion. The increase in firing rate is proportional to the difficulty, with the easiest trials increasing spike rate faster. Solid lines are in the preferred direction and dashed lines are the anti-referred direction. Shaded inset shows average responses from direction selective neurons in area MT to

motion in the preferred and anti-preferred directions. Right: Firing rates, aligned to eye movement. D: Firing rates of LIP neurons aligned on movement onset grouped by reaction times. Only the activities in the preferred direction are shown.

1.2.6 Modeling the DV

Tasks like random dot motion discrimination are interesting because they allow the researcher to control the amount of noise interfering with the evidence. Less coherence means that the net motion is harder to perceive and errors are more likely (Figure 1.1b). This feature parallels the uncertainty that comes with most decisions. In everyday life, we rarely have perfect information about every detail that might affect our decisions, and outcomes are almost never certain. This is even more so at the neuron level, where spiking activity also appears to have a significant level of randomness or noise. To model the evolution of a DV during a decision in this noisy environment, scientists have combined signal detection theory (Parker and Newsome 1998) and sequential analysis with probabilistically weighted evidence. This class of model is often referred to as a diffusion model initially described by Ratcliff (Ratcliff 1978, Gold and Shadlen 2007).

1.2.7 Diffusion models

Diffusion models have received increasing attention from the neuroscience community for their ability to model the behavioral and neural data related to fast, two-choice decision making. In these models, evidence about a stimulus or memory (which can be thought as the DV) builds up towards one of two thresholds. Each threshold represents the amount of evidence necessary to commit to one of the two choices offered to the subject. The setting of the threshold can be conceptualized as the implementation of a decision rule. The accumulation of evidence is noisy: at any point in time, the accumulation of evidence might favor attaining one threshold versus the other, but ultimately one choice will be favored. The noise introduces a variability in reaction time from trial to trial, creating a distribution of reaction times across trials. The main parameters that influence the shape of this distribution are the rate of accumulation of evidence (drift rate) and the setting of the thresholds.

Many versions of diffusion models have been successfully fitted to a variety of experimental observations including recordings in different brain regions across various tasks and sensual modalities (van Veen, Krug et al. 2008, Bogacz, Wagenmakers et al. 2010, Mulder, Keuken et al. 2013). In particular, convincing support for the drift-diffusion models has come from modelling the speed accuracy trade-off (Ratcliff and Rouder 1998) in tasks where decisions are made under speed pressure and faster reaction times increase the error rates. Diffusion models have also been applied to human behavioral data (Palmer, Huk et al. 2005) as well as neuroimaging studies (Forstmann, Dutilh et al. 2008).

Although they do not provide direct evidence for specific decision-making mechanisms, these computational models do provide a framework for studying the neuronal representation of a decision rule. Giving instructions that emphasize speed over accuracy for example increases the drift-rate and lowers the threshold (Wagenmakers, Ratcliff et al. 2008, Vandekerckhove, Tuerlinckx et al. 2011). Others have also used the model to investigate the priors that inform the decision rule in the context of value-based decisions (Forstmann, Brown et al. 2010).

In conclusion, studies in perceptual decision-making were crucial in expanding our understanding of decisions by showing how areas not typically involved in cognition are also involved in the decision process by being informed of what is important for an upcoming decision. Those studies were also instrumental to the development of computational models that could describe the comparison of options as a competition to a spiking threshold at the neural level.

However, while these are powerful models, they are limited to relatively fast decisions governed by a simple decision rule which begs the question: how can these models be expanded to include the decisions we encounter in our day-to-day life? For example, is the same mechanism used when deciding between completely different tasks with different modalities and rules? How can one be approaching a threshold for one action when one is already engaged in performing another? While these questions remain unanswered, some insight can be obtained by studying the last part of the decision: the action resulting from a choice.

1.3 Embodied decisions

1.3.1 General Description

The conceptual approaches to decision making discussed above are entirely focused on what happens before a decision is reached. When the subject has made-up his/her mind, the decision is translated into action. Embodied choice, however, considers that the actions are part of the decision process and influence the outcome. Action selection and preparation help specify choices and the dynamics of the action itself influences the choice made. For this reason, embodied decisions are studied in tasks where decision leads to movement and focus on neural representations of decisions in motor areas of the brain.

Similar to what has been observed in gaze control regions, neural recordings in non-human primates from the primary motor cortex (M1) and premotor cortex show that these areas are also involved in the build-up toward a decision threshold (Cisek and Kalaska 2005, Thura and Cisek 2014, Peixoto, Kiani et al. 2018). In forced two-choice perceptual decision tasks, neuron populations tuned to arm movements aligned with the different reach directions of the choice targets exhibit activities that ramp up together until the activity for one target wins, resolving the competition prior to the initiation of movement (Coallier and Kalaska 2014, Thura and Cisek 2014, Coallier, Michelet et al. 2015). Behavioral experiments in humans have also shown that the motor system tracks the evolution of the DV during deliberation. For example, in a random-dot motion task where subjects indicate their choice with an arm movement, perturbation of the arm at random times during the decision process produces a reflex that is modulated by the coherence and direction of the dot motion (Selen, Shadlen et al. 2012).

However, this competition between actions has not necessarily been resolved before the initiation of the movement. When subjects are faced with rapid but uncertain decision scenarios involving a reaching movement, the early trajectory of the hand often follows a middle ground between the two possible targets or initially launches towards one choice before later correcting for the other. Recent studies (Chapman, Gallivan et al. 2010) have even shown that the “averaged” initial trajectories reflect a probabilistic average based on the number and location of the targets.

1.3.2 Perturbations

Other results in support of embodied decision-making can be found in studies of movement perturbations. In a typical perturbation task, a reaching movement by the subject is perturbed by exerting a force on the arm pushing it away from a reach target. These studies have repeatedly shown how adaptable the motor plans formulated for goal directed behavior are: within less than 100ms the arm muscles’ stretch response reflexively fight the perturbation and the motor plan is adjusted to compensate and reach the target. These experiments can also reveal the flexibility of those plans. In another variant of these experiments, multiple reach targets are presented to the subject. This lets the subjects choose an initial target at the beginning of their reaching movement, but they could still redirect their reaches towards a closer alternative target after being perturbed or avoiding an obstacle (Nashed, Crevecoeur et al. 2014). Collectively these observations suggest that the motor plans are constantly updated, adapted and sensitive to new opportunities that arise, ready to switch the goal of a movement as it is happening.

1.3.3 Movement dynamics

Another way that the motor system influences decisions is through the dynamics of a movement. For example, during a reaching task, the biomechanics of the arm favor movements towards the body midline as they are less effortful, which is reflected in the subject’s preferences (Morel, Ulbrich et al. 2017). Other recent studies even showed that this bias takes into account the entire planned movement, as the stopping cost and endpoint stability also affect a subject’s choices (Cos, Bélanger et al. 2011, Cos, Medleg et al. 2012).

For example in one such study, the biomechanics of the arm moving on a plane are modeled using the torques at the shoulder and the elbow. This setup shows that movements of the cursor mainly involving the elbow joint are less costly than movements that must implicate the shoulder joint. A human subject is tasked with moving a cursor on a digitizing tablet toward one of two targets. This movement must be made by guiding the cursor through a via-point. The via-points are positioned such that the launching biomechanical cost of the movement is equivalent in both directions, but the end of the movements (from via-point to target) are of lower cost for one target and higher cost for the other.

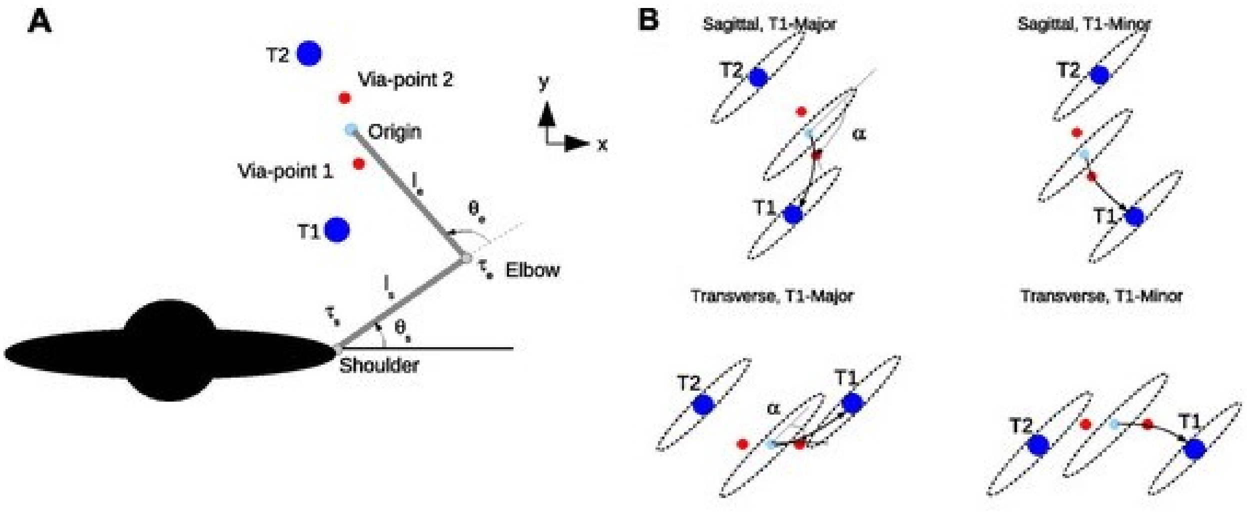


Figure 1.2 Depiction of task used (Cos, Bélanger et al. 2011) to demonstrate the influence of biomechanics on decision-making A: Schematic representation of the experimental setup. The arm of the subject is suspended in a flat plane and is modeled as a two-segment rigid body rotating around two joints (shoulder and elbow). Red dots are the via-points, and blue dots represent targets (T1, T2). B: Depiction of the planar stimulus arrangements. The ellipses show a qualitative display of mobility, or the ease of movement starting at the center of the ellipses. Note that the launching trajectory from origin to via-points 1 or 2 is equivalent in terms of alignment with the axes of that ellipse, but arrival trajectory to T1 or T2 is follows the long axis for one target and the short axis for the other. In “T1-Major” arrangements, a movement to T1 arrives along the major axis of the ellipse signifying an “easier” movement (requiring lower overall torques). In contrast, movements to T2 in that arrangement arrive along the minor axis and necessitate higher torques and are thus “harder”.

The results of that study show that subjects are much more likely to choose the targets when they are in the major-arrival arrangement then when they are in the minor-arrival arrangement, implying that the biomechanics of the movement are influencing the subject’s decision (Cos, Bélanger et al. 2011). This finding has been replicated in a number of studies in humans involving different tasks. Notably, a bias for easier/lower cost movement degraded performance in a random dot motion discrimination task (Marcos, Cos et al. 2015). This bias could be viewed in economic terms as the cost for an action, where effort and stability are priors calculated in sensorimotor areas that weigh on the decision as it is deliberated.

1.3.4 Navigation

As decision studies started to investigate the contribution of motor areas of the brain to decision-making, the field began to overlap with motor-control. Studies in motor control are often more concerned with how we perform an action than which action we choose to perform. However, as discussed in the previous paragraphs, those two facets of acting aren’t easily separated. How we achieve our goals informs our options and vice-versa.

Probably the most studied system of motor control is the control of the locomotion. While much of the locomotion system is sub-cortical, the cortex is necessary for navigating a natural environment like a forest, where perceptual information is required to inform foot placement on uneven ground and to avoid obstacles. Notably the posterior parietal cortex (PPC) seems to be critically important for visually guided navigation. Studies in cats show that the activity of PPC neurons is sensitive to the relative position of obstacles and the gait cycle (Drew and Marigold 2015). The activation of these cells is also context dependent, with increases in firing rates observed while a subject is traversing specific parts of a route (Sato, Sakata et al. 2006, Sato, Sakata et al. 2010). In short, the PPC appears to contribute to the creation of our egocentric spatial reference frame, allowing us to navigate complex environments.

In locomotion and other motor control studies however, the favored models are based on control systems. A continuous feedback between perceptual evidence, motor plans and movements is updated and fine-tuned in real time. This contrasts the decision-making paradigm of accumulator or attractor models reaching a threshold. Given the influence of motor control on decision making and the similarity between some navigation tasks and perceptual decision-making tasks, could some decisions be better modeled within a control systems framework? The affordance competition hypothesis attempts to conceptualize decision processes as similar to control systems: a continuous loop where perceptions and potential actions are used to guide a subject to its goals.

1.4 Affordance competition hypothesis

Key insights about the decision systems in our brain can be gained by studying their evolutionary history. Given that the neuroanatomical structures of the brain are remarkably conserved throughout vertebrate evolutionary history, our decision systems are likely heavily based on those of the simpler organisms from which we descended. In those organisms, decisions were geared toward pragmatic behavior such as seeking food, finding a mate, or evading predators. Most of these decisions need to be made in response to a continuous perceptual stream of the environment in order to be able to react in real time to threats and opportunities. To be adaptable, the decision-making circuitry can't be focused on predetermined binary outcomes, or on specific features of perception like in a typical laboratory setting. Rather, it must be prepared to execute several possible actions and simultaneously examine many sensory features to continuously guide behavior.

The affordance competition hypothesis (Cisek 2007) proposes that the processes of action selection and specification occur simultaneously and continuously, even while engaged in an action. In other words, the sensory information stream combines with internal stimuli to specify several currently available potential actions, termed "affordances" (Gibson 1979). As in diffusion and other accumulator models, these affordances compete until one is selected and guides behavior.

However, in the affordance competition hypothesis, the competition is strongly shaped by the context of the subject. As these affordances represent potential action plans, they are highly sensitive to the geometry of the environment and the biomechanics involved in their execution. Specifying potential actions necessitates a strong temporal component, especially in a changing environment or if the subject is moving. It's also likely inherently shaped by the current activity one is engaged in. For example, a hockey player's current momentum must be taken into account when he decides how to act in response to opposing player's movement. Similarly, a prey might decide to hide when it spots a predator while close to stationary, but instead to flee if already in motion. This raises interesting questions as to how our actions shape the landscape of our affordances (Lepora and Pezzulo 2015, Pezzulo and Cisek 2016).

1.5 Deciding while acting

The lab experiments described above in the various approaches to decision-making are quite far from natural decision-making in our regular lives. One aspect that stands out particularly when compared to real life is that subjects are all in a passive initial state. They're not moving and are simply waiting to get to the next trial. From this motionless state, they are presented with a choice, they decide and finally act on their decision. This is strikingly different from many decisions in our busy lives. Many decisions that we perform daily, such as going to get coffee also involves interrupting the task we are currently doing, or altering our route through the campus. Since we are seldom idle and waiting for new opportunities to choose, we are almost constantly deciding to either maintain a current course of action or switch to a new one. We have to decide while we are acting.

Studies of embodied decision-making already provide some insights into the adaptability of motor plans. They can be altered in real time to account for obstacles and changing information, and in doing so, they can influence the decision-making process. In particular, several studies have shown that decisions can be made "in flight" as subjects head between targets prior to knowing which one is correct (Chapman, Gallivan et al. 2010, Gallivan, Chapman et al. 2011, Gallivan, Chapman et al. 2018) or when unexpectedly perturbed (Nashed, Crevecoeur et al. 2014). However, in these studies the subjects only have one particular goal, and the adjustments are directed to achieve this singular goal. This is reflected in the neural activity of sensorimotor regions as they emphasize or de-emphasize certain stimuli and movements. What, then, happens when those same regions are already engaged in the control of behavior and must consider the options of pursuing alternate goals? If the deliberation between pursuing different goals takes place in the same areas of the brain as the ones involved in the pursuit of the current goal, the system of decision making must be capable of some level of parallel processing, or a way to quickly (in a fraction of a second) shift between alternatives.

This poses some problems for the current models of decision making. Notably, it highlights the constraints of the diffusion models. While the data clearly support an accumulation to threshold within in our brains, what then becomes of this threshold once action is initiated? Presumably, the neural populations of the FEF engaged in processing the stimuli or directing gaze to a decision-critical part of the field of view, would already be past some threshold of activity for the subject to act and perform this gaze shift. How can the same population then be involved in a parallel accumulation to threshold involving the pursuit of an alternate goal? If we consider that the regions involved in performing the competing actions are central to this build-up, then they would necessarily also be part of the competition in a subject deliberating between continuing to act on his current goal versus switching to another.

Deciding while acting also has interesting implications when related to the findings of embodied decisions. It has already been shown that the actions resulting from a decision can impact the outcome of that decision, and that the dynamics of movement are parts of the determinants influencing choice. It stands to reason that being engaged in an action could similarly bias the outcome of a decision. Being already engaged in movement could also limit the potential actions that are being considered by the brain, especially if stopping or losing balance or coordination results in high costs or high risks. This could open the door for the involvement of new motor areas and a more prominent role of motor areas in the decision-making process.

This deciding-while-acting task paradigm is what inspired the experiment discussed here. The aim was to design a task in which subjects were constantly involved in an activity, and while they were performing that activity, presented with a choice. From the outset we chose a task involving simple arm movements as some decision-making literature analyzing reaching movements, hand trajectories and arm dynamics could serve as a base of comparison. We quickly settled on a simple target tracking task as the main activity our subjects would be continuously performing. Then we added new potential “choice” targets for our subjects to track. This framed the choice as between “continuing” with the current target or “switching” to the new one. Importantly, the subjects had to deliberate while they were still tracking.

This task paradigm can be used to challenge the current theories of decision-making discussed above. For instance, do decisions taken while in motion rely on the same kind of common currency of value studied in neuroeconomics, or is this type of decision determined by the factors relating to the execution of the movement? Are the frontal brain areas involved in valuations of choices recruited during such a task, and if so, do decisions during action also follow the economic tenets such as choice transitivity of preference? Economic decisions made during movement might allow us to reveal new determinants of choice, or biases in the way we value decisions that require us to stop and change what we are currently doing.

Similarly, deciding-while-acting could shed more light on the process of accumulation to a decision threshold. Can this model be used to interpret decision-related activity for our task? The threshold is often presented as an initiation threshold, but in the case where a subject is already moving, a different interpretation is necessary. Recording neural populations in the relevant sensory areas and motor areas might elucidate how those competitions are resolved differently according to the context. Are those decisions done by resolving 2 competitions (one for stopping or not, another for selecting which target to track)? Are the competitions different and at different levels of the sensorimotor stream? One could hypothesize that the activity in visual areas might resemble what is observed in typical perceptual decision experiments, but that the activity in motor areas is dominated by control for the current movement and that only changes once the choice is already made.

This last point also raises the question of how do motor areas influence the decision as posited by the affordance competition hypothesis. Since neural resources must be devoted to controlling the action currently being performed, how does the brain allocate neural resources to consider the alternative affordances? Does the deliberation interfere with the ongoing movement? To what extent does the ongoing movement shape the landscape of affordances?

This task design was not aimed at answering all of the questions posed above. Rather, by introducing variations in some parameters of the task, such as the distance at which the target appears, the angle relative to the direction of motion or the size of the choice target we aimed to generate data on the behavior of human subjects that were deciding while acting and compare it to behavior in similar decide-then-act tasks. We hope that future, more comprehensive models of decision-making can address our data and incorporate choices that are made while performing another action.

2.0 Chapter 2: Reaching decisions during ongoing movements

Published as: Michalski, J., Green, A. M., & Cisek, P. (2020). Reaching decisions during ongoing movements. *Journal of Neurophysiology* 123(3), 1090-1102.

2.1 Abstract

Neurophysiological studies suggest that when decisions are made between concrete actions, the selection process involves a competition between potential actions representations in the same sensorimotor structures involved in executing those actions. However, it is unclear how such models can explain situations, often encountered during natural behavior, in which we make decisions while we are already engaged in performing an action. Does the process of deliberation characterized in classical studies of decision-making proceed the same way when subjects are deciding while already acting? In the present study, human subjects continuously tracked a target moving in the horizontal plane, and were occasionally presented with a new target to which they could freely choose to switch at any time, whereupon it became the new tracked target. We found that the probability of choosing to switch increased with decreasing distance to the new target and increasing size of the new target relative to the tracked target, as well as when the direction to the new target was aligned (either toward or opposite) to the current tracking direction. However, contrary to our expectations, subjects did not choose targets that minimized the energetic costs of execution, as calculated by a biomechanical model of the arm. When the constraints of continuous tracking were removed in variants of the task involving point-to-point movements, the expected preference for lower cost choices was seen. These results are discussed in the context of current theories of nested feedback control, internal models of forward dynamics, and high-dimensional neural spaces.

New and newsworthy

Current theories of decision-making primarily address how subjects make decisions before executing selected actions. However, in our daily lives we often make decisions while already performing some action (e.g. while playing a sport or navigating through a crowd). To gain insight into how current theories can be extended to such “decide-while-

acting" scenarios, here we examined human decisions during continuous manual tracking, and found some intriguing departures from how decisions are made in classical "decide-then-act" paradigms.

2.2 Introduction

In our daily lives, we are faced with a wide variety of decision-making scenarios. Some decisions are purely abstract, such as choosing which courses to take during one's university studies. These can be described as choices between representations of the costs and benefits of different predicted outcomes in a common currency of subjective utility (Rangel, Camerer et al. 2008, Padoa-Schioppa 2011, Levy and Glimcher 2012). Other decisions are more mundane and concrete, such as choosing where to sit when entering a classroom (Cisek and Pastor-Bernier 2014). Such "embodied decisions" can be thought of as involving selection between different potential actions, or what Gibson (1979) called "affordances". In that scenario, the potential actions are directly specified by sensory information about the geometry of the world, and selection between them can take place through a biased competition between internal representations of potential movements (Erlhagen and Schoner 2002, Cisek 2007, Gold and Shadlen 2007), which may be biased by their required effort (Cos, Belanger et al. 2011, Shadmehr, Huang et al. 2016, Morel, Ulbrich et al. 2017). Psychological and neurophysiological experiments on decision-making often combine aspects of both of these types of decisions by asking subjects to make a choice, about a percept or an estimate of value, and then report it with an action, such as a reaching movement or a saccade. Numerous studies have shown that when the actions used to report different choices are known to the subject ahead of time, the deliberation process is reflected in the sensorimotor regions responsible for guiding the movement – i.e. in the reaching network for reach decisions (Cisek and Kalaska 2005, Cui and Andersen 2007, Scherberger and Andersen 2007, Pesaran, Nelson et al. 2008, Andersen and Cui 2009, Westendorff, Klaes et al. 2010, Klaes, Westendorff et al. 2011, Pastor-Bernier and Cisek 2011, Thura and Cisek 2014, Christopoulos, Bonaiuto et al. 2015, Christopoulos, Kagan et al. 2018) and in the oculomotor network for saccade choices (Platt and Glimcher 1999, Gold and Shadlen 2000, McPeek and Keller 2002, Roitman and Shadlen 2002, Ditterich, Mazurek et al. 2003, Huk and Shadlen 2005, Gold and Shadlen 2007). This makes sense from an ecological perspective, which suggests that the brain evolved first and foremost to govern our interaction with the environment (e.g. selecting where to sit) and only much later elaborated its mechanisms toward abstract decision-making scenarios (e.g. selecting a university curriculum) (Pezzulo and Castelfranchi 2009, Cisek and Kalaska 2010, Engel, Maye et al. 2013, Cisek and Pastor-Bernier 2014, Pezzulo and Cisek 2016).

Nevertheless, even studies explicitly aimed at understanding how the brain selects between concrete actions have not fully addressed the complexities of real embodied decisions. In particular, they have primarily used what one may call "decide-then-act" paradigms, in which subjects are completely motionless during deliberation and make a movement only after committing to their final choice. Such tasks have led to the development of a diverse class of models which suggest that decisions are made when neural activity selective for a given act reaches a threshold, at which time movement is initiated (Stone 1960, Laming 1968, Ratcliff 1978, Hanes and Schall 1996, Usher and McClelland 2001, Mazurek, Roitman et al. 2003, Bogacz, Brown et al. 2006, Ratcliff and McKoon 2008, Cisek, Puskas et al. 2009, Thura, Beauregard-Racine et al. 2012, Carland, Marcos et al. 2016).

However, in our daily lives we often make decisions while we're already moving, such as when navigating through a crowd of students all struggling to get to different classrooms on time. In this scenario, each person is already performing an action, continuously adjusting it through feedback, all the while remaining sensitive to new potential options that may present themselves. The decision is between continuing to perform the current action versus switching to a new one, and requires one to continuously weigh the relative desirability of available options. If our theories of the neural mechanisms of embodied decision-making are to apply to natural behavior in the real world, they should be able to address these kinds of "decide-while-acting" scenarios. This presents a challenge to models that describe the transition between deliberation and commitment as the crossing of a neural threshold (Stone 1960, Laming 1968, Ratcliff 1978, Hanes and Schall 1996, Usher and McClelland 2001, Mazurek, Roitman et al. 2003, Bogacz, Brown et al. 2006, Ratcliff and McKoon 2008, Cisek, Puskas et al. 2009, Thura, Beauregard-Racine et al. 2012, Carland, Marcos et al. 2016) or entering an attractor (Grossberg 1973, Amari 1977, Wang 2002, Cisek 2006), because whatever group of cells is responsible for the ongoing action must already be past its threshold (or the system must already be within its attractor). Nevertheless, the system as a whole must still be capable of specifying alternative options and implementing a process of deliberation between continuing the current action versus switching to another. Furthermore, if a decision unfolds within the same brain regions that control ongoing actions (Erlhagen and Schoner 2002, Cisek 2007, Gold and Shadlen 2007, Klaes, Schneegans et al. 2012), then how can one deliberate about switching without interfering with the ongoing action?

Recent studies have examined situations in which reaching movements are initiated before decision commitment is complete. These have shown that deliberation influences the trajectory, at least during the early part of the action, and can even be used as a window into cognitive processes (Farmer, Cargill et al. 2007, McKinstry, Dale et al. 2008, Song and Nakayama 2008, Song and Nakayama 2009, Chapman, Gallivan et al. 2010, Gallivan, Chapman et al. 2011, Wood, Gallivan et al. 2011, Gallivan, Chapman et al. 2018). Other studies have shown that subjects can be externally induced to change their trajectory choices by a physical perturbation applied during a movement (Nashed, Crevecoeur et al. 2014). However, to our knowledge no study has examined how a subject who is already committed and fully engaged in performing some action can voluntarily deliberate about switching to an alternative action without interfering with the ongoing movement. It is this type of scenario that is most challenging for current models.

Here, we investigated decision-making during ongoing action control through behavioral experiments in human subjects performing a planar manual task. Our goal was to test which factors shown to influence choices during standard “decide-then-act” paradigms influence choices during a “decide-while-acting” paradigm. To maintain precise control over the kinematic and kinetic variables of interest, we asked subjects to continuously track a target with their hand while other potential choice targets were presented and subjects were free to either continue tracking the current target or switch to the new one. Tracking direction and choice target placement were designed to independently control spatial factors such as target distance, direction, and size, and kinetic factors such as biomechanical cost (in terms of average muscle torque). To provide a link to standard decide-then-act paradigms, we also tested subjects in a discontinuous version of the task in which all movements were point-to-point, as well as in a standard delayed reach decision task. Based on previous studies (Cos, Belanger et al. 2011, Cos, Medleg et al. 2012, Morel, Ulbrich et al. 2017), we predicted that subjects would show preferences for switching to near targets rather than far ones, to large targets rather than small ones, to targets well aligned with the current movement direction, and to directions incurring lower biomechanical costs. Some of these results have previously appeared in abstract form (Michalski and Cisek 2017, Michalski, Green et al. 2018).

2.3 Materials and methods

2.3.1 Subjects and apparatus

Twenty two right-handed subjects (7 men, 15 women) participated in the study. They had no known neurological disorders and had normal or corrected to normal vision, and all were naïve about the purpose of these experiments. They all provided written informed consent before the experimental session was initiated, and received a payment of $25/session for their participation. The protocol was approved by the Human Research Ethics Committee of the Faculté de Médicine, Université de Montréal.

The task apparatus consisted of a 91cm x 61cm digitizing tablet (GTCO Calcomp IV, Columbia, MD) in the horizontal plane, and a half-silvered mirror suspended 16cm above and parallel to the digitizer. Visual stimuli were projected onto the mirror by an LCD monitor suspended 16cm above, producing the illusion that the targets lie on the plane of the digitizing tablet. Subjects used their right hand to make movements using a digitizing stylus whose position was sampled at 125 Hz with a spatial resolution of 0.013cm. Subjects were seated in front of the task apparatus with their right shoulder aligned to the center of the screen and with their right arm resting in a sling supporting it just above the elbow. The sling was 107cm long and was positioned so that the anchor point was approximately directly above the subject’s elbow when they held the pen in the center of the screen.

2.3.2 Behavioral tasks

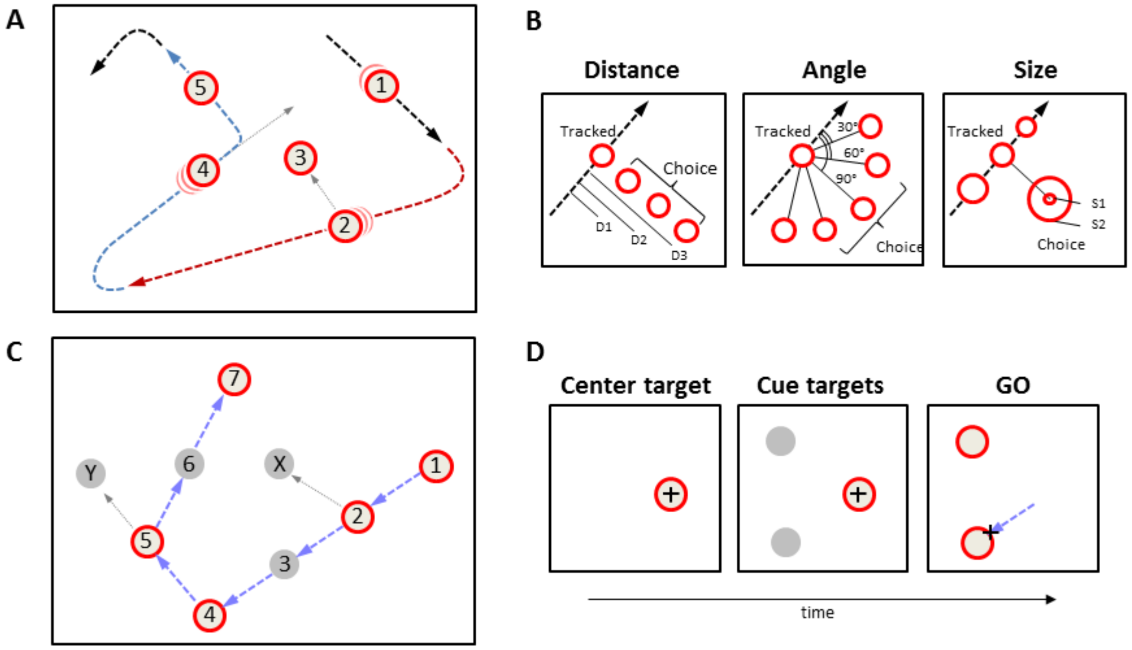


Figure 2.1 Behavioral tasks. A. An example schematizing the continuous tracking task. The subject's hand (dashed line) follows a "tracked target" (white circle with a red border), which moves around the screen at 6 cm/s. In the actual display, only the circle and a cross indicating hand position are visible. When the tracked target is at point 2, a "choice target" appears (circle 3), offering a potential new movement (gray dotted arrow) but the subject ignores it and continues to track the current target. At point 4, a new choice target appears (circle 5) and the subject switches to it, so it now becomes the new tracked target. Here, individual "trials" are defined by the colored segments, each of which presents the subject with a single decision scenario, and dotted gray lines indicate the options not taken. B. Three variations of the continuous tracking task. In the "distance block", the choice target always appears in a direction orthogonal to the current tracking direction but at 5 different distances (only three shown here). In the "angle block", the target always appears at a distance of 4.8cm but at one of 5 angles with respect to the current tracking direction. In the "size block", the tracked target is gradually shrinking and the choice target always appears orthogonal to the current tracking direction and at a distance of 4.8cm, but can be either larger or smaller than the currently tracked target. C. The discontinuous tracking task. Here, the tracked target (red circle) jumps by 4.8cm every 900ms and the subject tracks it with point-to-point movements. At time 1, the next target (2) is displayed along with two gray circles (3 & X) foreshadowing future targets. These turn red (not shown) 900ms after the subject moves into target 2. Now, the subject can make a choice and in this example, chooses to go to target 3, which is "aligned" with the previous point-to-point movement. At time 5, the subject chooses to go to target 6, which is "unaligned" with the previous point-to-point movement. D. The replay task. Here, the task is broken into individual trials, each starting when the subject places the cursor in the red circle, at which time two cues appear (gray circles). After 900ms they turn red indicating the GO signal, when the subject can freely choose either target. Importantly, the placement of the start and target circles is a replay of choice scenarios previously experienced when performing the discontinuous tracking task (here, from time 2 in panel C).

Continuous Tracking task (Figure 2.1a): Each experimental session consisted of an average of 80 “runs” of continuous tracking for about a minute each. At the start of each run, a luminous target (white with red border, 1cm radius) is projected on a black background. When the stylus enters the target, it begins to move, accelerating over 1 second to a constant speed of 6 cm/s that is maintained as long as the stylus is within the circle. This “tracked target” moves in a straight line until it reaches the edge of the workspace, where it gradually changes direction (either clockwise or counter-clockwise in a path along the circumference of a 1.5cm radius circle) until it begins to head in a new direction toward the central region of the screen. While the tracked target is passing through the central region, the subject is presented with a stationary “choice target” that remains available for 1400±200ms. The subject can choose to ignore this choice target and continue tracking the tracked target – we call this a “no switch” trial. Alternatively, the subject can choose to move the stylus into the choice target, whereupon the abandoned tracked target disappears while the choice target accelerates over 1 second to move at a constant speed in the same direction as the trajectory of the hand as it enters, and thus becomes the new tracked target. We call this a “switch” trial. The time at which the cursor starts to move towards the choice target (i.e., switching time) was defined as the first time (between choice appearance and tracked target exit) at which the distance to the target began consistently decreasing at a rate of more than 3cm/s. This time was obtained by starting at the moment the cursor exited the currently tracked target (i.e., when the rate of decrease had already exceeded the 3cm/s threshold) and going backwards in time until we found a time point at which the rate of decrease in distance to the choice target dropped below 3cm/s. The interval between choice target appearance and the switching time is defined as the “Switch Reaction Time” (SRT).

The task continues in this fashion so that the subject is always either continuously tracking the current target or switching to a new choice target. Whenever the currently tracked target reaches the edge of the screen, we define this moment as the end of a “trial” and the beginning of the next trial. Each continuous “run” consists of several trials without interruptions for approximately 1 minute, after which the subjects get an opportunity to briefly rest before starting the next run. Subjects are given a five minute period to practice the task after which they are instructed to keep going for blocks of 30 minutes.

Within each trial, the position at which the choice target appears depends on the type of block type currently being performed (Figure 2.1b). Pilot studies determined that in all three block types, the mean SRT was approximately 500ms. The choice target's position is thus determined based on where the tracked target will be 500ms after the choice target appears. In the "distance block" (Figure 2.1b, left), the choice target appears perpendicular to the direction of motion at one of five possible distances (2.4, 4.8, 7.2, 9.6 or 12cm). In the "angle block" (Figure 2.1b, center), the choice target appears at a 4.8cm distance, at one of five possible angles (30, 60, 90, 120 or 150 degrees) relative to the direction of motion. In the "size block" (Figure 2.1b, right), the tracked target is shrinking in size from its initial radius (e.g. 1cm for the first target of a run) to a minimum radius of 0.6cm at a rate of 0.3mm/s. Each choice target appears perpendicular to the direction of motion and at 4.8cm, but its radius is a value between 0.6cm and 1.2cm. Thus, the choice target is sometimes larger and sometimes smaller than the currently tracked target. If the choice target is entered, it becomes the new tracked target, and immediately begins to shrink in size, until it is abandoned in favor of a new choice target or the run ends. If the tracked target reaches a minimum radius of 0.6cm, it stops shrinking but continues to move around the screen.

In all conditions, subjects were instructed to follow the motion of the tracked target and to stay within the white circle as long as possible, but they were allowed to freely choose to switch to a different target if one appeared. They were explicitly told that the choice whether to switch or not was completely up to them and that as long as they were tracking a target, it didn't matter whether it was the old or new one. While it may seem that there's no reason for a subject to ever switch, in fact they did so quite often, allowing us to quantify the influence of the various factors that we manipulated (distance, size, etc.).

Discontinuous Tracking task (Figure 2.1c): This task is conceptually similar to the continuous tracking task, except that it involves a series of point-to-point movements instead of smooth continuous tracking. When the stylus moves into the "tracked" target, there is a 900ms delay and then the target disappears while a new target appears 4.8cm away. That target remains available until the subject enters it, and then after 900ms it also disappears and another new target appears. Thus, the subject makes a series of point-to-point movements approximately every 900ms. Tracked targets are presented in the same direction as the last movement unless reaching the edge of the screen, at which point they turn around. After reaching the edge of the screen, there are at least two jumps before a choice scenario ("trial") begins (although these are not depicted in Figure 2.1c). At the start of each choice scenario, when the new tracked target location is presented, two dim cues also appear simultaneously indicating the future choices. One dim cue represents the position of the next tracked target, 4.8cm away from the current tracked target and in the same direction as the previous movement. The second dim cue is positioned where the alternative target will be, 4.8cm away from the current tracked target and in one of 4 directions with respect to the workspace (45, 135, 225 or 315 degrees, where 0 is to the right). The angle of separation between the two dim cues was forced to be between 45° and 135° and in most cases was in the 60-120° range. Once the stylus reaches the tracked target, the dim cues are replaced with white targets with red borders, representing the next "tracked target" (aligned with previous motion) and the "choice target" (unaligned with previous motion), and the subject is free to choose to move to either of these. Subjects are required to wait for the targets to turn red, which can be considered equivalent to a "GO signal" in standard delayed reaching tasks (Kalaska and Crammond 1995).

We presented the dim cues in order to make both of the future target positions equally predictable well ahead of the time the subject would have to make their choice. This was motivated by pilot studies in which no such dim cues were presented, and subjects were just shown two white circles with red borders upon entering the tracked target. In that scenario, one of the circles was always in a highly predictable location (4.8cm away and aligned with the previous movement) while the other could be in one of many locations, and we found that subjects showed an overwhelming preference to choose the predictable target. Thus, because we wished to study the influence of factors other than target predictability, such as biomechanical costs, we chose to make the position of both targets is fully and equally predictable by presenting the dim cues ahead of the time of the choice.

Replay task (Figure 2.1d): In the discontinuous tracking task, subjects make decisions in the context of a sequence of movements. To compare these to decisions made outside of the context of a sequence, we presented subjects with a "replay" of the decision scenarios they encountered in the discontinuous tracking task, using the same spatial targets, but in separate independent trials each similar to classic instructed delay reaching tasks. In the replay task, the subject starts each trial by moving the cursor into an initial target, and then 2 gray choice targets appear 4.8cm from the initial one. After 900ms, the targets turn white (with a red border) indicating the GO signal, and the subject then moves the cursor to one of the 2 choices, ending the trial. In the 67% of subjects that performed the discontinuous task before the replay task, the positions of the initial target and the 2 choice targets were taken from the decision scenarios encountered during the discontinuous tracking task. Thus, these trials recreated the same decision scenarios that the subject faced in the discontinuous tracking task in terms of spatial locations and angular separations, but in a shuffled order and without the element of continuity between decisions. In 33% of subjects, the first block of the replay task was run before any blocks of discontinuous tracking, using the discontinuous session of a previous subject to determine target placements. Because behavior was the same in these replay blocks as those based on the subject's own performance (i.e. there was no effect of block order), we analyze all of these together.

2.3.3 Biomechanical modeling

For each trial, we used a biomechanical model to estimate the net torque produced by muscles during a period from 500ms before target onset to 1000ms after target onset. The model was built using the SimMechanics package within the SIMULINK simulation environment in MATLAB. The upper arm and forearm+hand limb segments were modeled as two thin rods with uniform mass distribution and average lengths and weight (males; upper arm: 30.9 cm, 2.1 kg; forearm+hand: 29.1 cm, 1.7 kg, females; upper arm: 28.6 cm 1.7 kg; forearm+hand: 25.8 cm, 1 kg) (Nikolova and Toshev 2007). The two limb segments were joined at the elbow with 1 rotational degree of freedom and the proximal upper arm segment was joined to a static body with 1 rotational degree of freedom. The model was constrained to a 2D horizontal plane.

The recorded positions of the stylus were interpolated at 100Hz using a 2D spline and filtered at 20Hz with a low-pass Butterworth filter (9th order) with zero delay. Velocity was computed using a five-point differentiation routine, and then both position and velocity were up-sampled to 1000Hz with linear interpolation and again low-pass filtered at 20Hz. Using inverse kinematics equations for a planar arm model, we calculated the angular position of each joint through time and then passed them through an inverse dynamics model (SimMechanics) to calculate the muscle torques produced at the shoulder and elbow joints.

We calculated the sum of the absolute muscle torques produced at both joints, averaged over a period of time meant to capture the cost of switching versus continuing. For switch trials, the average torque was calculated from 100ms before the time of the switch to 100ms after the cursor entered the choice target. For no-switch trials, average torque was calculated from 400ms after choice target onset (this corresponds to approximately 100ms before the average time that subjects normally switch to a choice target, which is 500ms as noted above) until the moment when the cursor reached the edge of the screen (before a change in tracking direction). Note that because no-switch trials involved a straight movement at a nearly constant speed, and thus nearly constant torque, the average torque calculation was not sensitive to the duration of the tracking or the precise window that was used. In discontinuous trials, average torque was calculated between the onset and offset of movement, each detected as 5% of peak movement speed. About 5.3% of trials in which onset and offset could not be clearly detected were excluded from this analysis.

As described below in the Results section, we found that some switches of direction during continuous tracking were more biomechanically costly than others, and this strongly depended on the angle from the cursor to the choice target (measured counter clockwise, where 0° is to the right). Consequently, we classified as “hard” those trials in which that angle was either between 286° and 15° or between 106° and 195°, and as “easy” those in which the angle was between 16° and 105° or between 196° and 285° (See Figure 2.3A).

2.3.4 Analyses of choice preferences

In the distance block of the continuous tracking task, we quantified the effect of distance by calculating the proportion of switch choices for each choice target distance, separately for easy and hard trials, and fit these with a sigmoidal curve described as $P_{switch}(X) = \frac{1}{1+e^{-a(X-b)}}$, where X is the distance to the choice target and a and b are the slope and the mean of the sigmoid, respectively. If distance has an effect, then we expect this sigmoid to have a negative slope. To test for significance of the distance effect, we computed 1000 sigmoids by randomly resampling the data (with replacement) across all subjects and if 97.5% of the distribution of parameter a was negative, we considered the effect of distance to be significant at $p<0.05$.

A similar approach was used to examine effects in the size block, except that here, X was defined as the difference between the choice target diameter and the tracked target diameter, trials were grouped into 9 bins according to X, and we tested for values of parameter a that were greater than zero (i.e. more switching to choice targets that are larger than the currently tracked target).

As described below in the results section, for the angle block subject choice preference curves were non-monotonic and so they could not be fitted with sigmoidal functions. Consequently, we fit the data with a 2nd order polynomial described as $P_{switch}(X) = a + bX + cX^2$, where X is the angle between the current tracking direction and the direction to the choice target. An angle effect was considered significant if the resampled distribution for either parameter b or c was different from zero.

To test for the effect of biomechanical costs in all three blocks (distance, angle, and size), we computed a distribution of the difference in the area under the curve (AUC) between biomechanically easy versus hard trials. This was done using a sigmoidal curve for distance and size blocks and a polynomial curve for the angle block. Next, to test for the significance of this difference, we constructed a distribution of 1000 differences after randomly resampling (with replacement) within each trial type. If zero lay outside the 95% confidence interval of this distribution then the effect of biomechanical costs was considered significant at $p<0.05$.

To test whether the proportion of switch choices depends on the current tracking direction or the direction to the choice target, we subdivided the circle into 30° bins, computed the proportion of switch choices within each bin, and performed a $\chi 2$ test to see if the switch choices were equally distributed across the bins. Results were considered significant at $p<0.05$.

2.4 Results

2.4.1 Behavior in the continuous tracking task

Eleven subjects performed the continuous tracking task, completing 747 trials on average (range 533-1013). Five of these subjects also participated in some pilot studies but their behavior in the final paradigm was no different than that of the remaining subjects, so their data was included. Figure 2.2 shows an excerpt of the cursor trajectory from an example session. During the trial highlighted in blue, the subject was moving to the upper right when a choice target (red circle) appeared 4.8cm to the left of the trajectory. The subject switched to this target after a 486ms Switch Reaction Time (SRT), whereupon it became the new tracked target and the task continued.

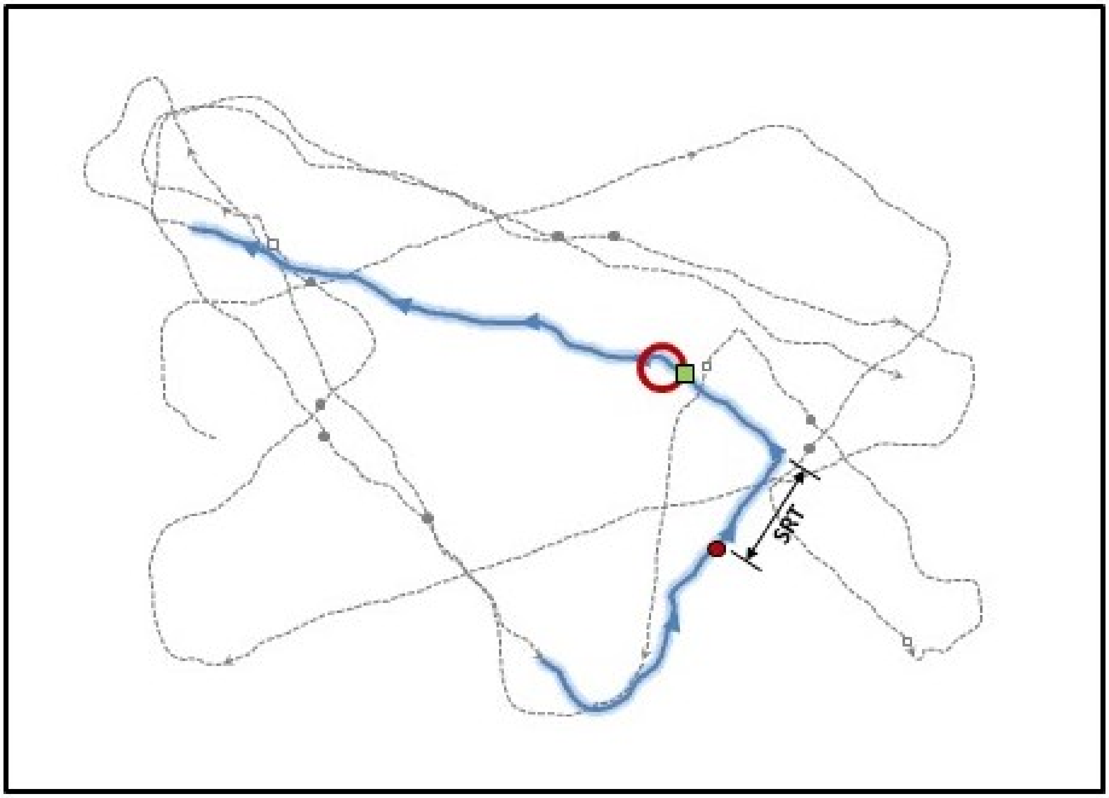
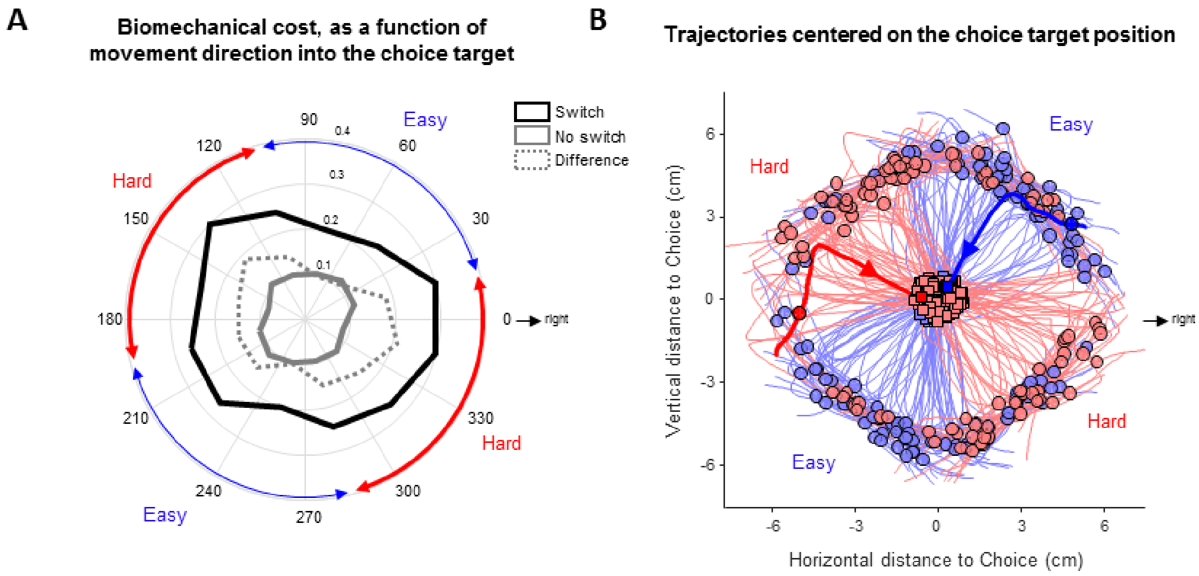


Figure 2.2 Hand trajectory (dashed gray line) from an example run of the continuous tracking task ("Distance" block). A single trial is highlighted in blue, with arrowheads indicating movement direction. The choice target (red circle) appeared at the moment the subject was at the position indicated by the red dot. After a short "switch reaction time" (SRT), the subject abandoned the tracked target, switched direction, and entered the choice target at the point indicated by the green square. Gray circles and open squares indicate analogous events in other trials within the same continuous run.

Across all subjects, the average SRT was 498ms (±168ms std), but it varied between the different blocks. SRTs were fastest in the angle block (median 457ms) and slowest in the size block (median 500ms) (Mann-Whitney U-test, $p<0.05$). Within each block, the differences between conditions (closer vs. farther, small vs. large angle, smaller vs. bigger radius) were negligible, although they reached significance in a few cases (e.g. fastest SRT when the choice target was 2.4cm away).

To examine whether presentation of a choice target and subsequent deliberation had any impact on movement kinematics, we examined the velocity and curvature of trajectories in trials in which a choice target was presented but subjects did not switch. The tangential velocity of tracking movements stayed close to the 6 cm/s speed of the tracked target (mean±s.d.: 6.04±1.85 cm/s). During trials in which subjects did not switch to the choice target, there was a 2.8% decrease in average velocity in a window 250-350ms after choice target appearance (to a mean velocity of 5.844 cm/s). This was significant when averaged across trials (p=0.0138) but it was not consistent in individual trials. Indeed, of the 1302 trials tested, the velocity 250-350ms after choice appearance was significantly slower than in the 100ms prior to the choice appearance in 637 (48%) of trials, but it was significantly faster in 586 (45%) of trials. Thus, we conclude that the slight reduction apparent in the average is not indicative of any consistent effect of deliberation processes on movement velocity. There was also no consistent effect of deliberation processes on the curvature of the trajectory, which remained straight throughout no-switch trials.



Biomechanical cost, as a function of movement direction into the choice target

Trajectories centered on the choice target position

Figure 2.3 Classification of trials into easy and hard bins in the continuous tracking task. A. Average cost of switching (black polygon, n=796 trials) versus continuing to track (gray polygon, n=1478), in trials where the choice target appeared at 90o to the current tracking direction. Cost is expressed in Newton-meters, averaged from choice target appearance until the time it was entered (switch trials) or until the screen edge was reached (no-switch trials), and plotted as a function of the movement direction (in absolute angles with respect to the workspace) to the choice target. The dotted gray polygon indicates the difference. Note that switching toward a choice target at 150° or 330° is more costly than switching to one at 60° or 240°. Hence, we define trials in which the choice target direction was in the range of angles marked in red as biomechanically “Hard” (n=1067), and those in which the choice target direction was in the range marked in blue as biomechanically “Easy” (n=1207). B. Sample segments of trajectories from switch trials, all aligned to the location of the choice target. Each segment begins 200ms before the choice appears (circle) and ends when the cursor enters the target (square). Segments are color coded according to the direction to the choice target, as defined in panel A (blue: easy, n=114; red: hard, n=104). Here, we include trials in which the choice target appeared 4.8cm away at 90° from the current tracking direction. Two example trials are highlighted.

The calculated biomechanical cost of switching versus continuing strongly depended upon the current tracking direction (Figure 2.3a). Switching to a transverse direction after moving in a sagittal direction was more costly than switching from transverse to sagittal directions. Consequently, we classified specific choice scenarios as “easy” or “hard” depending on the angle between the cursor and the choice target (See methods). Figure 2.3b shows excerpts of trajectories (all aligned on the position of the choice target) from individual trials in which a subject performed an easy or hard switch during the distance block of the task, with choice targets at a distance of 4.8cm. Across blocks, SRTs were not significantly different to biomechanically easy than hard choice targets (median 485ms vs. 489ms, MWU p=0.761).

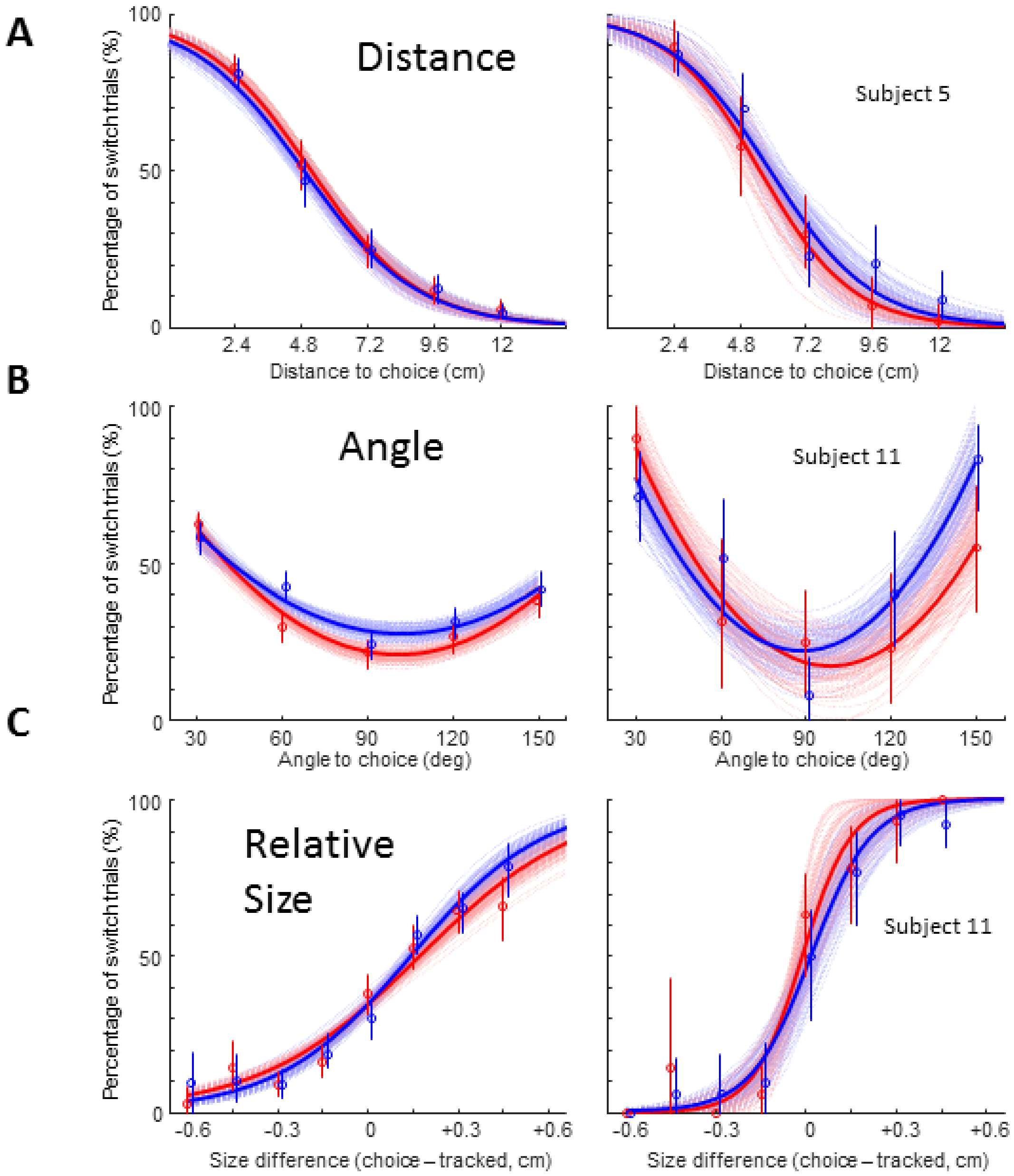


Figure 2.4 The percentage of switch choices, as a function of different task variables in each block of the continuous tracking task. Left column: All subjects; Right column: Example subject. A. Switch choice percentage as a function of target distance (Left: 5 subjects, n=2319 trials; Right: 1 subject, n=557 trials). B. Switch choice percentage as a function of target angle with respect to current tracking direction (Left: 11 subjects, n=3676 trials; Right: 1 subject, n=237). C. Switch choice percentage as a function of the radius of the choice target relative to the tracked target (choice minus tracked, in cm) (Left: 11 subjects, n=2973 trials; Right: 1 subject, n=320). Red:

Hard trials; Blue: Easy trials. Each panel shows a fit to the data (thick line) as well as 100 fits obtained after resampling the data with replacement (thin curves). Vertical lines indicate confidence intervals calculated by resampling.

Figure 2.4 shows the percentage of switch trials when subjects were faced with different kinds of choices. In the distance block (Figure 2.4a), subjects exhibited the expected preference for choice targets that were close over choice targets that were distant ($a<0$, resampling test $p<0.001$, see Materials and methods). However, there was no difference in the percentage of switch trials to a choice target that was biomechanically easy versus hard (AUC easy-hard=0, resampling test $p>0.170$).

In the angle block (Figure 2.4b), subjects switched more often when the choice target was closely aligned with the current tracking trajectory (30° or 60°) than when it was orthogonal (90°), and interestingly, they also chose to switch more often to targets oriented at large angles (120° and 150°) than at 90°. In other words, they tended to prefer choice targets in directions that lay along the current movement direction (even backwards) over choice targets oriented orthogonally ($c>0$, resampling test $p<0.001$). At the group level, there was also a mild preference for biomechanically easy choices (AUC easy-hard>0, $p=0.002$).

Finally, in the size block (Figure 2.4c), subjects chose to switch to the choice target more often when it was larger than the currently tracked target ($a>0$, resampling test, $p<0.001$). The point of subjective equality (when the switch choice was made 50% of the time) differed for individual subjects but at the group level it averaged out to 0.15cm. These choice preferences were not significantly different between biomechanically easy and hard trials (AUC easy-hard=0, $p>0.201$).

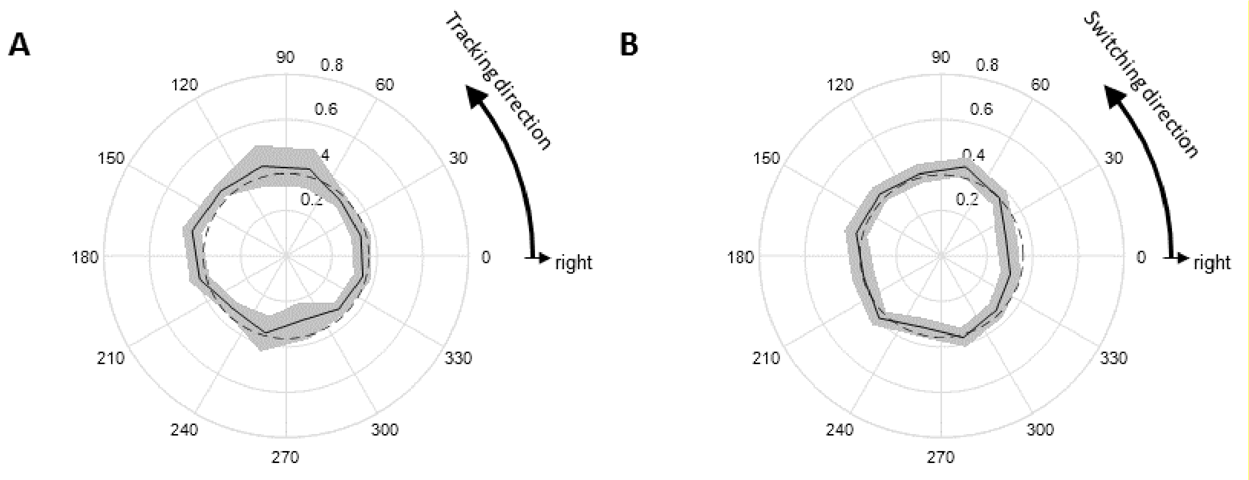


Figure 2.5 Percentage of switch choices made to the choice target during the continuous tracking task (solid line) as compared to a uniform circle (dashed). Shaded areas indicate the 95% confidence interval computed using the Clopper-Pearson method. A. The percentage is plotted as a function of the ongoing tracking direction (in absolute angles w.r.t. the workspace) at the time the choice target appeared. B. The percentage is plotted as a function of the direction to the choice target. In both panels, only trials where the choice target was oriented at 90° to the current tracking direction are included (n=5971 trials).

Subject choice preferences were remarkably similar across directions. For example, the probability of switching to a choice target at 90° to the currently tracked direction was approximately 35% across all tracking directions. When the percentage of switch trials was plotted as a function of the current tracking direction (Figure 2.5a), there was a small but significant deviation from uniformity (χ2 test, p=0.0171). Notably, however, when the percentage of switch trials was plotted as a function of the direction to the choice target, it was not significantly different from uniformity (Figure 2.5b, χ2 test, p=0.207). This was surprising because it contrasts with the anisotropy of the biomechanical costs of switching, shown in Figure 2.3a.

2.4.2 Behavior in the discontinuous tracking task

Fifteen subjects performed the discontinuous tracking task, completing 407 trials on average (range 334-594). Because there was a GO signal in this task, and movements occurred on a 900ms rhythm, reaction times were much shorter (approximately 250ms) than the SRTs in the continuous tracking task. This is presumably because the pre-cues allowed the subjects to make their choice well ahead of time, as in classic instructed delay tasks with a GO signal. On average, RTs were slightly faster when subjects chose the aligned target than when they chose the unaligned target (median 245ms vs 261ms, MWU p<0.001).

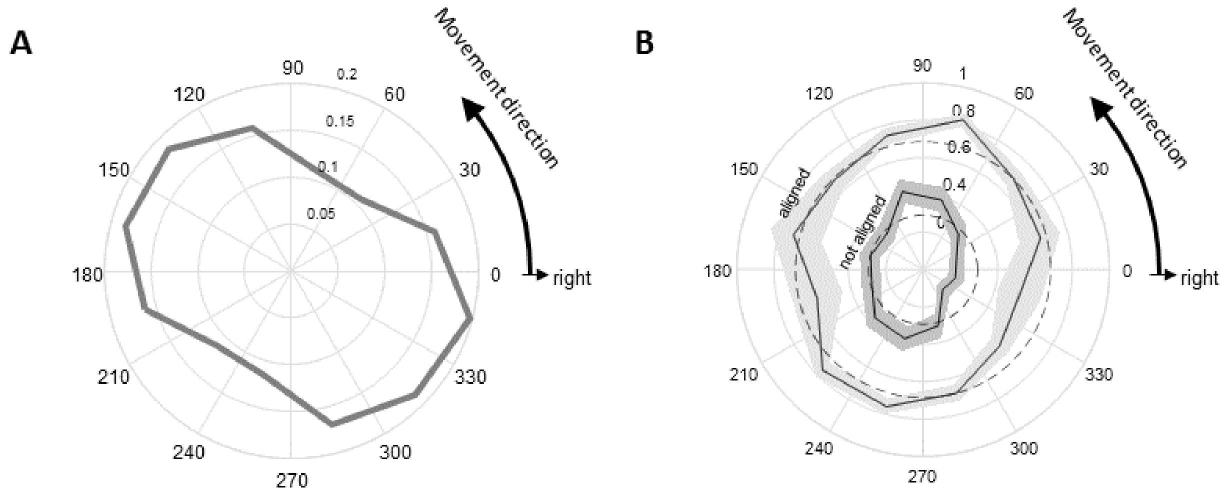


Figure 2.6 Data from the discontinuous tracking task. A. Calculated cost (in Newton-meters) of moving to a target as a function of the direction to that target (n=3019 trials). Note that, similarly to Figure 2.3A, the plot implies that there is a greater cost in moving to a target oriented at 150° or 330°. B. Outer polygon: The probability of selecting a target that is aligned to the previous movement, as a function of the direction to that target (n=2159). Inner polygon: The probability of selecting a target that is not aligned with the previous movement, as a function of the direction to that target (n=860). Solid lines indicate means, shaded areas indicate confidence intervals (computed as in Figure 2.5), and dashed circles indicate a uniform distribution.

Figure 2.6a shows the biomechanical cost of point-to-point movements during the discontinuous tracking task as a function of movement direction. As expected, this has an ellipsoidal shape that is similar in orientation to the cost of making a switch in the continuous tracking task (Figure 2.3a, blue). Figure 2.6b shows the percentage of choices made, during the discontinuous tracking task, as a function of the direction to the chosen target, for targets that were aligned (red) versus unaligned (blue) with the previous movement. First, note that although subjects made a full stop between each point-to-point movement, the percentage of choices is higher toward targets aligned with the previous point-to-point movement (red) than to targets that are not aligned (blue) (χ2 test, p<1x10-100). Furthermore, the pattern is significantly non-isotropic, with more choices made to targets in sagittal directions than transverse directions both when the target is aligned (χ2 test, p=0.012) or unaligned (χ2 test, p=2.68x10-12). This is consistent with the pattern of biomechanical costs shown in Figure 2.6a. In other words, in the discontinuous tracking task subject exhibited a preference for targets aligned to their previous movement, as well as a smaller but significant preference for targets in directions of lower biomechanical costs.

2.4.3 Behavior in the replay task

All of the subjects who performed the discontinuous tracking task also performed the replay task. As in the discontinuous tracking task, subjects were given a predictable GO signal, and consequently their RTs were short (approximately 200ms), slightly shorter than in the discontinuous tracking task (MWU, p=0.0072).

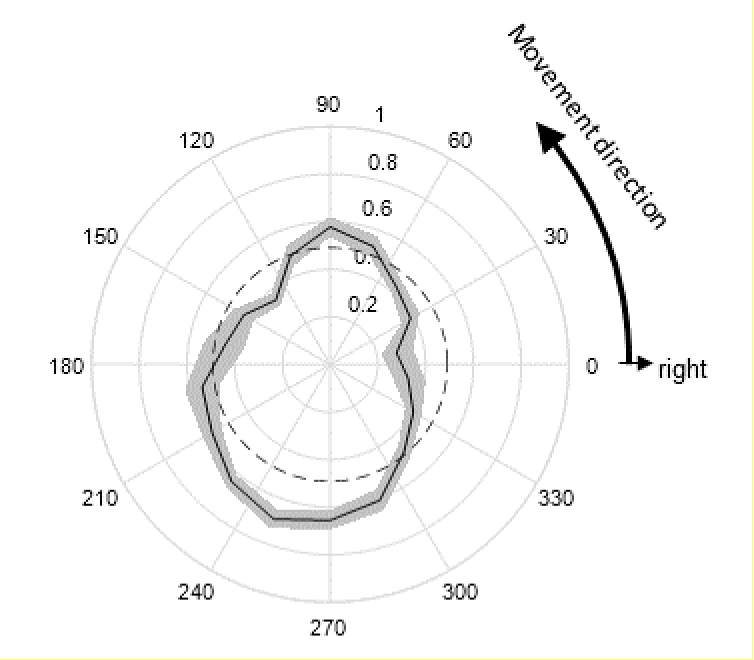


Figure 2.7 Data from the replay task. Probability of selecting a target as a function of the movement direction to that target (n=4523 trials). The solid line indicates the mean, the shaded area indicates confidence intervals (computed as in Figure 2.5), and the dashed circle indicates a uniform distribution.

To examine the effect of biomechanical costs outside of the context of a sequence of movements, we replayed (in a random order) the choice scenarios that subjects previously experienced in the discontinuous tracking task, this time in a standard design of individual and independent point-to-point reach decision trials. As shown in Figure 2.7, subjects chose targets in the biomechanically easier sagittal directions significantly more often than targets in the biomechanically harder transverse directions (χ2 test, p=0.0100).

There was also a slight but significant preference for targets toward the body (χ2 test, p=0.0032).

2.4.4 Comparison of biomechanical costs of tracking, switching, and point-to-point movements

As shown above (Figure 2.4), in the continuous tracking task we found that choice preferences were strongly influenced by target distance, angle, and relative size, but not by the biomechanical cost of movements. This is in contrast to our findings in the other tasks (Figure 2.6b, 2.7), in which choices were significantly biased toward the biomechanically easier movements. One potential reason for this could be due to the different torque demands of performing continuous tracking versus point-to-point movements. To examine this question, we compared the distribution of biomechanical costs (average arm muscle torque, see Methods) of three kinds of trials: point-to-point movements during the discontinuous tracking task; no-switch trials in the continuous tracking task; and switch trials in the continuous tracking task.

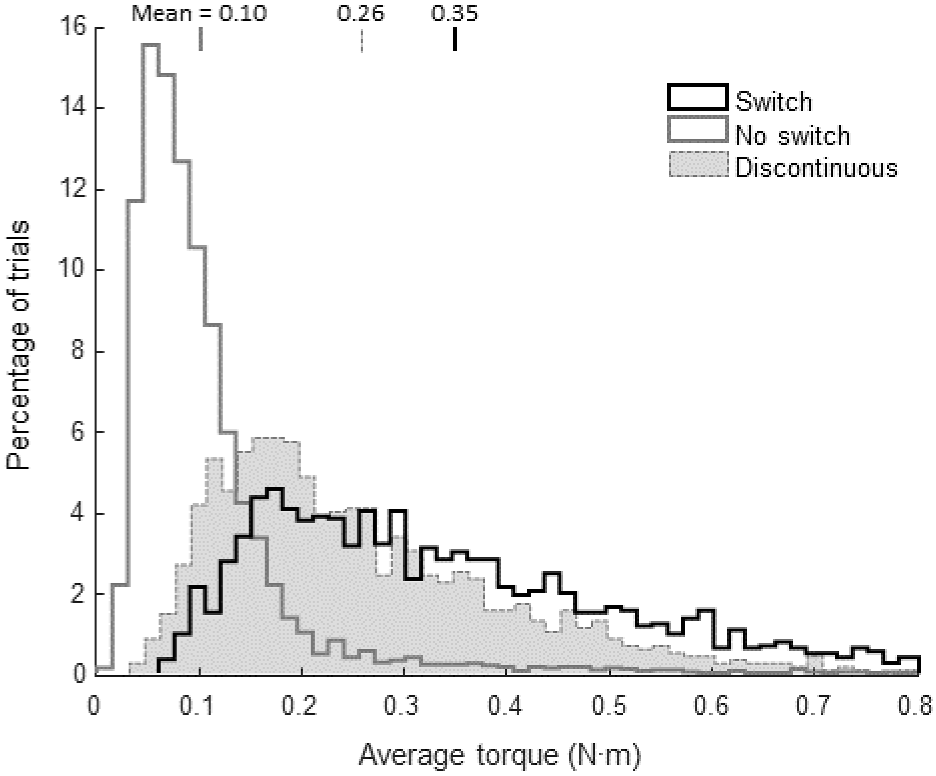


Figure 2.8 Distributions of biomechanical costs for different kinds of movements (in Newton-meters), computed as the sum of the absolute shoulder and elbow muscle torques averaged across time (see Methods). Black: Continuous tracking task when the subject switched to the choice target (n=2144 trials). Gray: Continuous tracking task when the choice target was ignored (n=3827). Dashed: Discontinuous tracking task (n=6108), resampled 100 times from each 30° bin of directions, to avoid biases caused by the anisotropy of subject choices. Small vertical lines above the plot indicate the means of each distribution

Figure 2.8 shows the resulting distributions. In solid black and gray are the histograms from switch and no-switch trials, respectively, during the continuous tracking task. In dashed line is a histogram of the biomechanical costs from the discontinuous tracking task. To prevent biasing the distribution to the lower cost choices that subjects tended to prefer (Figure 2.6b), this distribution was calculated using an equal number of 100 randomly sampled movements from each 30° bin of movement directions.

As expected, the average cost of switching movements is higher than the cost of continued tracking. Furthermore, the cost of the movements made when switching targets is similar, but slightly higher than the cost of point-to-point movements during the discontinuous task (MWU test, p<1x10-36). This could be partially attributed to the fact that movements made when switching tended to be faster than movements made during discontinuous tracking, and partially to the necessity to slow down before changing direction. Most importantly, however, one cannot conclude that subjects ignore biomechanical costs during continuous tracking (Figure 2.4) because those costs are so low as to be negligible, since a similar range of biomechanical costs does appear to influence their decisions during the discontinuous tracking task (Figure 2.6b).

2.5 Discussion

Neurophysiological studies conducted over the last few decades often show decision-related modulations of neural activity in many brain regions commonly associated with the execution of movements (for reviews, see Gold and Shadlen 2007, Andersen and Cui 2009, Cisek and Kalaska 2010). Even when choices are about perceptual discriminations or reward value comparisons, as long as the response actions are known, the decision process appears to engage neural activity in the regions associated with those actions – e.g. saccade regions for eye movements (Platt and Glimcher 1999, Gold and Shadlen 2000, McPeek and Keller 2002, Roitman and Shadlen 2002, Ditterich, Mazurek et al. 2003, Huk and Shadlen 2005, Gold and Shadlen 2007, Bennur and Gold 2011), reach regions for decisions about arm movement (Cisek and Kalaska 2005, Cui and Andersen 2007, Scherberger and Andersen 2007, Pesaran, Nelson et al. 2008, Andersen and Cui 2009, Westendorff, Klaes et al. 2010, Klaes, Westendorff et al. 2011, Pastor-Bernier and Cisek 2011, Thura and Cisek 2014, Christopoulos, Bonaiuto et al. 2015, Christopoulos, Kagan et al. 2018), or grasp regions for decisions about grip types (Baumann, Fluet et al. 2009). Behavioral studies reveal congruent results – if decisions between reach choices must be made quickly, sometimes even after movement begins, then reach trajectories often start in-between the targets, as if two motor “plans” or “goals” are being mixed (Chapman, Gallivan et al. 2010, Wood, Gallivan et al. 2011, Gallivan, Logan et al. 2016, Gallivan, Chapman et al. 2018); (but see Haith, Huberdeau et al. 2015).

However, in many natural situations humans and other animals must make decisions while they are already engaged in complex activity, and cannot allow those decisions to interfere with the ongoing action. For example, while running away from a fox, a rabbit can consider a variety of escape routes that may reveal themselves as the chase unfolds. However, while it deliberates about these possibilities, it must not allow the deliberation to interfere with ongoing foot placement, obstacle avoidance, etc. Models suggesting that decisions unfold within the circuits controlling action (Erlhagen and Schoner 2002, Cisek 2007, Gold and Shadlen 2007, Cisek and Kalaska 2010, Klaes, Schneegans et al. 2012) must confront this challenge – how can decisions unfold in the same neural system controlling an action without interfering with that action?

In this study, we sought to examine what kinds of factors bear upon decisions made during ongoing manual tracking behavior. Our long-term goal is to examine whether models of action selection developed on the basis of standard “decide-then-act” paradigms can generalize to situations in which decisions must be made while already acting. This question is relevant both to models described at a behavioral level (Ratcliff 1978, Busemeyer and Townsend 1993, Ratcliff and McKoon 2008, Cisek, Puskas et al. 2009) as well as to models of the neural mechanisms (Grossberg 1973, Amari 1977, Wang 2002, Mazurek, Roitman et al. 2003, Cisek 2006), especially ones that define commitment as the crossing of an initiation threshold or falling into an attractor. To characterize the constraints for such models, the specific goal of this study was to determine which of the factors that influence choices during standard “decide-then-act” tasks also influence choices during “decide-while-acting” tasks. In particular, we looked for the influence of target distance, target size, target direction with respect to current movement, and the relative biomechanical cost of switching versus continuing to track the target.

Although there was no explicit reason for subjects to switch to the choice target, they in fact did so quite often. This allowed us to quantify how the probability of switching varied as a function of the kinematic and kinetic factors that we manipulated. As expected, we found that subjects chose to switch to a new target more often when it was close to the current tracking target and less often when it appeared far away (Figure 2.4a). Also as expected, subjects preferred to switch to targets that were larger in size than the currently tracked target, although they did sometimes switch when it was slightly smaller (Figure 2.4c). These results are in agreement with previous studies on free choice reaching tasks (Cos, Belanger et al. 2011, Cos, Medleg et al. 2012, Cos, Duque et al. 2014, Morel, Ulbrich et al. 2017) as well as with a recent study showing both size and distance preferences in human subjects performing a "foraging task" involving reaching movements to targets on a plane (Diamond, Wolpert et al. 2017).

Somewhat more surprising was the pattern of choices as a function of the angle between the choice target and the current tracking movement (Figure 2.4b): subjects tended to switch often when the angle was small, least often when it was orthogonal, and then again slightly more often when the choice was behind the tracked target, requiring a movement in a nearly opposite direction. One possible explanation for this result implicates the recruitment of muscle synergies (Domkin, Laczko et al. 2002, d'Avella and Bizzi 2005, Tresch and Jarc 2009). A tracking movement requires the activation of agonist muscles that move the arm in the tracked direction as well as some engagement of antagonist muscles that stabilize the cursor within the target and ensure accurate velocity matching (Engel and Soechting 2000). Thus, a synergy of muscles acting both along and against the current movement vector are already engaged and controlled during manual tracking. By contrast, muscle groups that act orthogonally to the current movement vector are not active. It is possible that switching from a currently used synergy to an orthogonally-acting one incurs some additional costs that reduce the desirability of targets in the orthogonal direction. It would be interesting to explore this possibility using analyses of muscle activity, but that was beyond the scope of the current study.

The most surprising result of our study, however, was the lack of a consistent influence of the biomechanical costs of movement on the decision to switch. Although an orthogonal turn from a movement at 45° to one at 135° required nearly 50% more muscle torque than the opposite orthogonal turn (Figure 2.3a), the observed choice preferences did not reflect that cost. The only case of a significant difference in choice preferences was a slight preference for the biomechanically easy target when averaging across all subjects in the angle block, primarily due to trials in which the choice target appeared at 60° (Figure 2.4b). In general, however, it does not appear that subjects made choices that minimized biomechanical costs. This is surprising given prior evidence that subjects can take biomechanical costs into account when selecting different point-to-point reaching movements (Cos, Belanger et al. 2011, Cos, Medleg et al. 2012), and do so within 200ms of target presentation and well before movement onset (Cos, Duque et al. 2014). It is also surprising given the growing theoretical motivation and empirical evidence that classical economic choices and energetic aspects of motor control may be treated by unified mechanisms aimed at maximizing a common measure of utility (Shadmehr, Huang et al. 2016, Morel, Ulbrich et al. 2017, Yoon, Geary et al. 2018, Carland, Thura et al. 2019).

This surprising result could potentially be explained if the differences in torque requirements were simply too small to be relevant to our subjects. As shown in Figure 2.8, however, the average torques of switch trials were comparable and indeed slightly higher than those encountered during the discontinuous task, in which clear preferences for movements with lower biomechanical cost were seen (Figure 2.6b). Nevertheless, it is possible that while biomechanical costs during continuous tracking were not negligible, their influence was dwarfed by all of the other factors that together determine a subject's behavioral success. In one of our previous studies of manual choices in a decide-then-act paradigm (Cos, Medleg et al. 2012), we found that the influence of biomechanical cost was strongest when subjects had the fewest constraints on their movement trajectory. In particular, the influence of biomechanics was strongest when choosing between wide, easy-to-hit targets without the requirement to stop in the chosen one. When the size of the targets was reduced, the effect of biomechanics was smaller. When subjects were instructed to stop in the target, the effect of biomechanics was reduced still further (though it was never completely absent). In other words, as subjects faced additional constraints in the movements they had to perform, the relative influence of biomechanical costs on their choice behavior was reduced. In the continuous tracking task studied here, subjects face still more constraints: They have to keep both the position and velocity of their hand matched to the position and velocity of the tracked target (Miall, Weir et al. 1993, Engel and Soechting 2000), requiring simultaneous visual tracking (Mather and Putchat 1983, Danion and Flanagan 2018). Success in the task is defined as meeting these constraints, whereas the choice to switch is completely free and arbitrary, so the energy expended may be less important. Indeed, when the demands of manual tracking are eased, as in the discontinuous tracking and replay tasks, biomechanical influences become stronger and more consistent with minimization of effort (Figures 2.6b and 2.7).

Another interesting observation is that the Switch Reaction Times of our subjects performing the continuous tracking task (median 490ms for a choice target at 90°) are in the normal range of reaction times for simple decisions in tasks where the target and GO signal are presented simultaneously (and thus do not allow preparation in advance). This suggests that subjects do not need substantial time to "disengage" from their current action so that they can plan a new one (although switching to a new target did take longer than the approximately 230ms latency to adjust one's trajectory when a tracked target unpredictably changes direction; (see Engel and Soechting 2000)). Nevertheless, the presentation of a potential choice during the ongoing tracking action did not appear to interfere with the performance of that action. While a slight tendency for tangential velocity to decrease after choice target presentation appeared when averaged across trials (see Results), this was not consistent in individual trials.

Importantly, the choices facing our subjects were not about switching between different kinds of activity (e.g. saccade versus reach) but were always about different movements made with the same effector – their right arm. Therefore, if the selection, planning and control of reaching is governed by activity on a map of potential actions (Erlhagen and Schoner 2002, Cisek 2006, Klaes, Schneegans et al. 2012), then our task forces the activity on that map to simultaneously control an ongoing movement while representing an alternative potential action. But if that alternative potential action competes with the ongoing movement, then how can it not interfere with its execution?

Two hypotheses seem plausible. First, it is possible that the competition between actions takes place in neural circuits that are separate from those controlling the ongoing movement. For example, ongoing movement control may be governed by primary motor and somatosensory cortex, which together comprise a tightly integrated "inner" circuit straddling the central sulcus (Jones, Coulter et al. 1978, Pandya and Yeterian 1985, Kalaska, Cohen et al. 1989, Bullock, Cisek et al. 1994, Johnson, Ferraina et al. 1996, Crammond and Kalaska 2000). In contrast, action selection may unfold independently in an "outer" circuit that includes the dorsal premotor cortex and medial intraparietal area (Johnson, Ferraina et al. 1996, Wise, Boussaoud et al. 1997, Crammond and Kalaska 2000, Andersen and Cui 2009, Westendorff, Klaes et al. 2010). Alternatively, all of these regions could govern ongoing control while target selection instead takes place in an abstract space of outcomes represented in still more rostral regions, including dorsolateral prefrontal cortex and other frontal lobe areas (Padoa-Schioppa 2011). In both cases, activity related to selection would need to be transmitted to sensorimotor circuits only at the time the new action was to be initiated. This does not explain, however, why biomechanical costs influence decision-making processes in decide-then-act situations. One potential explanation could be that when subjects make decisions while stationary, sensorimotor circuits play a role in computing the biomechanical costs of potential movements and this information is transmitted back to the circuit involved in selection (Lepora and Pezzulo 2015). As long as such sensorimotor circuit activity remained below the threshold for causing changes in muscle activity it would not interfere with ongoing postural maintenance. In contrast, during ongoing movement, sensorimotor circuits might simply be too "busy" with the task of online control to provide information about biomechanical costs to decision-making processes.

A second hypothesis is made possible by the high dimensionality of the space spanned by the millions of neurons in all of these regions. High dimensionality implies that any given movement can be redundantly specified and identically controlled by a very wide variety of neural activity patterns that define an "output-potent" subspace. Similarly, there are many combinations of activity patterns which don't influence a given motor action, and these define an "output-null" subspace for that action (Kaufman, Churchland et al. 2014). In mathematical terms, the two subspaces are orthogonal, as recently suggested for motor cortical populations controlling different arms (Ames and Churchland 2019). However, different activity patterns within a given action's output-null subspace can lie closer or farther from the set of neural activity patterns that makes up an output-potent subspace for controlling a different action. This means that the decision to switch could unfold as a shift of the neural activity pattern, always within the null subspace orthogonal to the ongoing action (or the ongoing maintenance of posture), yet moving increasingly toward the subspace of a new action being considered. Only when the neural activity pattern crosses over into the output-potent subspace of the new action does a switch in behavior occur. If the subspace in which deliberation takes place in decide-then-act tasks is quite different from that in which it takes place during an ongoing action this might help to explain why in our study biomechanical costs did not appear to influence choices during ongoing action despite influencing choices when the initial state is stationary (Fig. 6 & 7, and Cos, Belanger et al. 2011). Note that the first hypothesis is a really special case of the second hypothesis – it is a particular case in which the two subspaces involve largely distinct neural populations.

Another explanation, not exclusive of the others, is that biomechanical costs of multiple potential actions can be computed by a cerebellar forward model during decide-then-act tasks (Bastian 2006, Pasalar, Roitman et al. 2006), but that during decide-while-acting tasks the circuit is too busy in controlling the ongoing action to predict the costs of a potential switching movement. This would predict that the cerebellum can represent multiple potential actions when an effector is at rest, but once a given action begins then only that one action can be processed.

Finally, an alternative interpretation of our results is that they are less related to whether deliberation occurs when the hand is at rest versus when moving and more indicative of differences in the kinds of variables required for controlling the different tasks we have explored. As noted above, continuous tracking requires subjects to control their velocity to match that of the tracked target, while maintaining the hand within a specific target location. Perhaps biomechanical costs are simply not very important in the face of such constraints. Furthermore, tracking movements may engage a different subset of cells from those primarily involved in point-to-point movements, such as switching to a new target. Perhaps cells involved in tracking are less sensitive to variables closely related to biomechanical costs (e.g. acceleration) than cells involved in point-to-point movements.

Answering such questions motivates future studies involving neural recordings in animals trained to perform tasks like the continuous tracking task. Though to our knowledge this type of paradigm has not yet been attempted in monkeys, potential insights may be found in data from studies in other species and other conditions. For example, studies in cats have examined situations in which the animal must choose, during ongoing locomotion, which forelimb to use to step over an obstacle (Drew and Marigold 2015). These studies suggest that cells in parietal cortex estimate the animal's position with respect to the obstacle while cells in motor cortex primarily contribute to the execution of the stepping movements and their modifications. In contrast, cells in premotor cortex appear related both to the execution of the gait modification as well as to the selection of the limb that will be used to step over it (Nakajima, Fortier-Lebel et al. 2019). Importantly, many premotor cells exhibit a gradual increase of discharge rate several steps prior to the gait modification. This is seen both in cells that are limb-independent and cells specific to a given forelimb, but no changes in EMG activity are observed until the final moment of gait modification. It therefore appears that at least in the cat locomotion system, it is possible for cells putatively involved in execution to also exhibit decision-related activity, even during ongoing actions. By analogy, for the primate reaching system one might therefore predict that during continuous tracking, cells in dorsal premotor cortex tuned to the direction of the choice target will begin to increase their activity as the subject is deliberating, and then either increase even more during switch trials or fall back to baseline in no-switch trials. Ultimately, neurophysiological studies of decide-while-acting paradigms will be required to shed light on these interesting questions.

2.6 Acknowledgements

The authors would like to thank Christophe Martin for assistance in the implementation of the biomechanical modeling. This work was supported by Discovery Grant (RGPIN/05245) from the Natural Sciences and Engineering Research Council (PC).

3.0 Chapter 3: Discussion

3.1 Motivation for the current study

Although recent research has started looking into embodied decisions, the majority of research on decision making still studies decisions and their resulting actions separately. Despite mounting evidence of the involvement of sensorimotor areas of the brain in the decision-making process, the methods almost always employ what we termed a decide-then-act paradigm. In this paradigm, scientists tend to only focus on what happens until movement onset, often using this event to mark the end of deliberation.

However, in many natural situations, agents have to make decisions while already engaged in an action. As an example, humans have to make many decisions while moving when they are playing sports such as deciding to whom and when to pass the ball while dribbling. Similarly, in the animal world, most hunts will involve several decisions that can have a big impact on the survival of predator or prey, leading us to suggest that the ability to make decisions while acting was selected for by natural selection and might have played an important role in shaping the decision-making systems of the brain.

In the present study, we wished to design a task using a decide-while-acting paradigm in which we could investigate some of the factors influencing decisions that have previously been identified in decide-then-act studies. Our goal was to contrast the two paradigms to see to what extent conclusions regarding those factors acquired from decide-then-act studies would still hold when subjects were moving as they were deciding. This fits into a broader goal of elucidating whether theories of action selection developed under the decide-the-act paradigm can be applied to the natural context of making decisions during ongoing action.

3.2 Results

We expected that some assumptions would be confirmed despite the subjects being engaged in an action while deciding. As discussed in the paper, subjects performing the task showed a preference for targets that were closer and bigger. This unsurprising result could be explained by a bias for lower biomechanical costs, as closer targets involve shorter reaches, and bigger targets are significantly easier to track than smaller ones. However, this could also be explained by a bias in visuo-spatial attention. If the subject's attention is mostly focused on the tracked target and ahead of it, closer targets are more likely to be attended to and in turn make a switch more likely. Similarly, bigger targets are more salient and thus more likely to capture the subject's attention. While our task does not allow us to discern precisely the cause of this preference, we were expecting it to hold during a decide-while-acting task based on previous observations in free choice tasks (Cos, Bélanger et al. 2011, Cos, Medleg et al. 2012, Morel, Ulbrich et al. 2017).

We also observed a preference for targets that were most closely aligned along the axis of movement. To our knowledge, this hasn't been observed previously, but could potentially be explained by the recruitment of muscle synergies (Domkin, Laczko et al. 2002, d'Avella and Bizzi 2005, Tresch and Jarc 2009). A tracking movement requires the activation of agonist muscles that move the arm in the tracked direction as well as some engagement of antagonist muscles that stabilize the cursor within the target and ensure accurate velocity matching (Engel and Soechting 2000). The observed preference could be linked to a preference to use the muscle groups already engaged in the motor control of the current movement. It is also possible that switching muscle groups involves additional costs at the muscle levels, but this was not assessed with our study.

The most interesting result was the lack of observed biomechanical bias in our continuous tracking task. In previous studies involving point to point arm reaches in a decide-then-act paradigm, subjects had been shown to favor movements which minimized muscle torques (Cos, Bélanger et al. 2011, Cos, Duque et al. 2014). We were able to replicate those results in our discontinuous tracking task by breaking the tracking into a series of point to point movements. However, during continuous tracking, when subjects had to decide while moving, they exhibited no preference for movements with lower biomechanical costs.

There could be a number of reasons for this. One possible explanation is that the continuous tracking task introduces other constraints on the movement (such as velocity matching) that are more important than and take precedence over any biomechanical bias. This is supported by a previous experiment that showed that adding constraints on movement, such as asking subjects to stop their movement in a small target area, decreased the preference for movements generating lower torques (Cos, Medleg et al. 2012).

Another possible reason why we didn't see a biomechanical bias in the continuous task might be that sensorimotor areas of the brain are too busy with controlling the current action, in this case tracking a target, to be able to model the biomechanical costs of potential actions. When subjects are offered a choice that must be realized by executing a specific action, neural activity in the sensorimotor regions related to enacting that action seems to reflect the decision process (Gold and Shadlen 2007, Cisek and Kalaska 2010). Perhaps this activity is a way for the brain to model potential actions and their associated biomechanical costs, among other variables of relevance to the considered movements. However, if the brain regions responsible for modeling arm movements are occupied with maintaining the tracking of a target during deliberation, they might not be able to estimate and compare the biomechanical cost of switching to a new target versus staying with the current one. This would imply that deciding while acting results in decisions that are less optimal, or incorporate a different set of biases in the decision process.

A third explanation is related to the task design. In our continuous tracking task, staying with the current target involved maintaining the smooth tracking of a target. The other possible choice, switching, involved a point-to-point movement. Those two types of movements have a few key differences. Tracking requires a constant velocity and involves constant hand-eye coordination (Engel and Soechting 2000) to correct any deviation. Point-to-point movements are characterized by a constantly changing velocity (acceleration then deceleration) and hand-eye coordination is mostly used to control the arrival at the destination. It is possible that the brain emphasizes different factors for those two type of movements. For example, point-to-point reaches have a well conserved and typical velocity profile regardless of direction or length. In this case, optimizing movements to reduce muscular torques might be prioritized. However, because tracking is much more stimulus-dependent, the brain might prioritize accuracy and precision in hand-eye coordination and never really model the potential biomechanical costs of tracking.

3.3 Limitations

This last point highlights a limitation in our task design. When analyzing the behavior of subjects performing the continuous tracking task, we were not able to find a logic to explain when and why subjects switch. The location of the tracked or choice target had no impact on probability of switching. Similarly the direction of movements before or after a switch did not reveal any directional preferences in the subjects. Our modeling of torques shows that switches generate on average higher torques than staying with the tracked target. Why then would the subject switch? For equal distance, target size or angle in relation to direction of motion, could the switching behavior be entirely random?

One of the limitations of our task relates to the motivation of the subjects. In most studies of goal-directed behavior, subjects are motivated by a reward. Typically, trials have a correct choice, yielding a small reward while the incorrect choice yields no reward or a penalty. An earlier version of our continuous tracking task actually incorporated a reward scheme. In this prototype version, the tracked target would be associated to a value indicated by the brightness of the target. For each second of successful tracking, this value would be added to a cumulative point total that would translate to a small increase of monetary reward at the end of a session. To discourage the subjects from always staying with the tracked target, this value would decrease over time, eventually reaching zero.

Since the targets lost value quickly and the difference in value between the tracked target and the choice target were small, we hypothesized that we would observe a higher likelihood of switching to higher or lower value targets in directions associated with lower torques. However, piloting with this version revealed that subjects only cared about value, to the extent of always switching when there was a higher value target presented, and never switching when the value was lower. Versions of the tasks with a value proposition were therefore abandoned in favor of a task where there was no “correct” choice, and reward was the same regardless of performance. We reasoned that subjects would be naturally motivated to avoid higher torques. To an extent this was true as we were able to observe a bias for movements generating lower torques in the discontinuous tracking task. However, torques remained small in all tasks, providing little incentive to optimize for lower torques.

Another limitation of our study is that it was designed based on decision-making variables previously shown to be relevant in point-to-point reaching tasks. However, direct comparisons between point-to-point and tracking tasks in terms of the determinants of choices may not be appropriate. For example, since a tracking movement is much more stimulus-dependent, it may be that the brain doesn't perform any modeling of the biomechanical cost of tracking and therefore this variable may be irrelevant to the decision process. Alternatively, biomechanical cost might simply have much less influence on decisions, so that its effect is only observable when other factors that might influence a decision are absent.

Related to this is the possibility that biomechanical costs are indeed calculated for different movement types, but that this calculation is more accurate for some types of movement as compared to others. Point-to-point reaches are highly stereotyped movements with kinematics that depend mostly on distance, which may enable the brain to predict costs efficiently and relatively accurately. On the other hand, the brain might model a rough estimate of the cost of a tracking movement that depends on how fast the target is moving and how long the subject is expected to track. However, in this scenario, because such variables are likely to be less well defined, cost estimates may in turn be less accurate and harder to compare across choices, especially when the costs are small, as in our task. These possibilities highlight the limitations of direct comparison of very different types of movement.

One way to improve on those limitations could be the use of an external exoskeleton such as the KINARM to constrain the movements of the subjects. In this apparatus, a relatively small maximal velocity (about the same as the tracking speed) could be imposed. The goal would be to constrain the velocity profile of the switching movement to be much closer to that of the tracking movement: quickly reaching a plateau and maintaining a constant speed. Additionally, using the KINARM, a resistance can be introduced to increase the force necessary to move the cursor. This would increase all the torques, which could provide subjects with a clearer assessment of what movements are more costly and a better motivation to minimize effort. A resistance would also eliminate stopping costs, which would simplify the calculation of torques. This KINARM version of our task could address some of the questions raised above. Notably, if a bias for lower torques is observed, it can be deduced that sensorimotor areas aren't too pre-occupied to model biomechanical costs, and that they do so when it is important to the task at hand.

3.4 Future Directions

Beyond simply improving on the limitations of our study, we think there is value in integrating the decide-while-acting paradigm into many of the typical studies of decision making to see if findings can be replicated. We believe such studies could help challenge and refine models of decision-making, as well as broaden their applicability to a wider range of natural scenarios. Below are a few suggestions of where this research could be taken.

3.4.1 Perturbations studies

Perturbations studies are one of the fields from which deciding while acting takes some of its inspiration. Most of these studies involve perturbing a movement during an action to see how subjects compensate, correct or adapt. Interestingly, it has already been shown that motor plans can be quickly adjusted to react to perturbation in ways that are sensitive to the goals of the subject (Nashed, Crevecoeur et al. 2012, Nashed, Crevecoeur et al. 2014). But none of those studies introduce perturbations during a choice. Could perturbation such as pushing the arm to one side affect the outcome of a decision on a tracking task? Can the corrective response to perturbations account for potential actions in addition to the one being performed? A positive response to both of those questions would yield support for the importance of the primary motor cortex in the outcome of decisions involving movement, since the corrections observed in the cited studies are thought to originate from M1 (Pruszynski, Kurtzer et al. 2011).

Another line of inquiry could be to test to what extent the perturbations can bias decisions. Moving through a crowd is a common scenario that can involve a high amount of perturbation to locomotion. One might find it preferable to employ a detour to avoid such disturbances, even at the risk of losing some reward. This kind of experiment would be interesting as it might shed light on the differences between decide-then-act and decide-while-acting situations. When considering an action from a resting state, the biomechanical cost might factor into the decision, but perhaps those costs aren't so important if already moving. Rather, precise control of the movement could be favored, as the rapid adaptation of motor plans suggests.

3.4.2 Galvanic vestibular stimulation

In addition to proprioceptive stimuli, feedback control during a movement also uses sensory information from other modalities, such as the vestibular system. Galvanic vestibular stimulation (GVS) allows researchers to induce an illusory whole-body rotation in the subject by exciting the vestibular afferents with an electric current (Fitzpatrick and Day 2004). This illusion interferes with reach movements, so subjects compensate for the illusory shift in the body's spatial orientation (Moreau-Debord, Martin et al. 2014) and these compensations are also task-dependent (Keyser, Medendorp et al. 2017). An interesting question would be to investigate whether this simulated motion perturbation induced by GVS not only influences ongoing movement but also new potential movement options. An experiment could be designed to have a subject moving their arm while they are presented with two potential reach targets. By timing the moment of the GVS pulse, one could test if the resulting compensation for the perturbation either reflects a prior decision about which target to reach to as well as whether it influences the decision itself. For example, imagine performing an ongoing movement while at the same time deciding whether to switch direction towards a target located to the left or to the right. If a GVS pulse is then applied during deliberation, will the direction of the compensatory movement induced by the GVS tend to deviate towards the target the subject was considering at the moment of the pulse? Alternatively, will the compensatory response itself tend to bias the choice to reach towards one target versus the other? Such modulations in response would suggest that potential actions are influenced by both the spatial and dynamic aspects of perceived body motion as signaled by the vestibular system.

3.4.3 Transcranial Magnetic Stimulation

Another way of non-invasively probing an evolving decision in the motor cortex is to measure motor-evoked potentials (MEPs) elicited by transcranial magnetic stimulation (TMS) (van Elswijk, Kleine et al. 2007, Klein-Flugge and Bestmann 2012). In a decide-then-act task, it was shown that the MEPs obtained early during the deliberation correlated with the choice behavior of the subject, whereas later MEPs were primarily related to the muscular requirements of the movement (Cos, Duque et al. 2014). It would be interesting to repeat a similar experiment in a decide-while-acting task to see if we can still observe subthreshold MEPs linked to the subject's deliberation. Since subjects are already moving when deliberation occurs, the MEPs, which are an indirect measure of cortico-spinal excitability, might only reflect the current movement, which could point to another difference between decide-then-act and decide-while-acting paradigms.

This also raises the question of whether cortico-spinal excitability can bias a decision. This excitability can be conceptualized as a preparation for an action. Does the brain favor movements that are prepared over newly arising motor plans? A bias favoring muscles that are already involved in the current movement could explain some of the results we observed in our task in the angle variant where subjects were more likely to switch to target situated in line with the axis of movement, either forward or backwards compared to those situated orthogonally to the direction of movement. However, to truly distinguish if such a bias is due to excitability in the efferent path, or to mainly cortical mechanisms, direct neural recordings would be needed.

3.4.4 Neural recordings

Neural recordings are perhaps the type of experiment that could most benefit from using a decide-while-acting paradigm. For instance, neural recordings during our experiment could help elucidate if the neural populations involved in manual target tracking are sensitive to different aspects of the stimuli compared to neurons involved in point-to-point reaches. If neurons engaged by tracking are more tuned to changes in velocity, while neurons involved in point-to-point reaches are more tuned to acceleration, this could provide a direct explanation for why torques factor into decisions in the discontinuous task (point-to-point), but have no effect in the continuous task (tracking). This would also add to the mounting evidence that the actions surrounding a decision are important to the decision process.

It would also be interesting to identify the populations of neurons whose activities relate to biomechanical cost. Studies have only just begun to identify neurons that are sensitive to effort and have found some in the anterior cingulate cortex (ACC) (Walton, Bannerman et al. 2003, Kennerley, Behrens et al. 2011), the midbrain (Croxson, Walton et al. 2009, Pasquereau and Turner 2013) and the primary motor cortex (Kalaska, Cohen et al. 1989, Takarada, Mima et al. 2014). Recordings of such neurons during a decide-while-acting task could reveal whether being involved in an action interferes with the computation of the effort associated with potential actions which could explain our findings.

In most neural recording experiments investigating decision-making, neural activity is interpreted as a competitive rise to a threshold and modeled with drift-diffusion or attractor models. However, it is unclear how and if such models could be applied to interpret neural activity during a decide-while-acting task. A first line of inquiry could be to investigate whether the same neural populations that are involved in the current movement are also implicated in this competition. If this is the case, how can those neurons achieve both online control and participate in the decision process simultaneously? A possible answer invokes the high dimensionality of the space spanned by the large number of neurons involved. High dimensionality implies that any movement is specified redundantly by a wide variety of neural activity patterns that define the “output-potent” subspace, but there is also an equally wide variety of neural activity patterns that do not interfere with the movement in an orthogonal “output-null” subspace (Kaufman, Churchland et al. 2014). A decision in which potential actions are considered could evolve within this output-null subspace without interfering with the ongoing action. As the competition is resolved, the neural activity could shift to be ever closer to the output-potent subspace until it crosses over into that subspace and the decision is enacted.

Rise to threshold models also suggest that a threshold has already been crossed for the subject to be moving. But does neural activity need to be maintained beyond this threshold to maintain an ongoing action? Presumably, any effortful activity must be winning the competition against stopping to be maintained. What then happens when subjects are presented with continuing an ongoing action versus switching to a different action? Does the ongoing action benefit from a head start on the competing action, reducing the amount of activity needed to reach the decision threshold? Neural recordings during a decide-while-acting task have the potential to address what happens in this interesting context and to either challenge or broaden our current models of decision-making.

3.5 Conclusion

As previously discussed in this text, recent research has shown how actions can be important to the decision-making process. Consequently, we believe that the path to understanding how animals choose involves further studies on how action control systems influence decisions, especially considering that the relationship between action and decision would have been central to the evolution of decision systems. We hope that the decide-while-acting experimental paradigms can be used in future studies to clarify this relationship and to broaden decision-making models to include more natural contexts.

4.0 Chapter 4: Reference List

Amari, S. (1977). "Dynamics of pattern formation in lateral-inhibition type neural fields." Biol Cybern **27**(2): 77-87.

Ames, K. C. and M. M. Churchland (2019). "Motor cortex signals for each arm are mixed across hemispheres and neurons yet partitioned within the population response." Elife **8**.

Andersen, R. A. and H. Cui (2009). "Intention, action planning, and decision making in parietal-frontal circuits." Neuron **63**(5): 568-583.

Bastian, A. J. (2006). "Learning to predict the future: the cerebellum adapts feedforward movement control." Current Opinion in Neurobiology **16**(6): 645-649.

Baumann, M. A., M. C. Fluet and H. Scherberger (2009). "Context-specific grasp movement representation in the macaque anterior intraparietal area." J Neurosci **29**(20): 6436-6448.

Bennur, S. and J. I. Gold (2011). "Distinct representations of a perceptual decision and the associated oculomotor plan in the monkey lateral intraparietal area." J Neurosci **31**(3): 913-921.

Bogacz, R., E. Brown, J. Moehlis, P. Holmes and J. D. Cohen (2006). "The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks." Psychol.Rev. **113**(4): 700-765.

Bogacz, R., E. J. Wagenmakers, B. U. Forstmann and S. Nieuwenhuis (2010). "The neural basis of the speed-accuracy tradeoff." Trends Neurosci **33**(1): 10-16.

Britten, K. H., W. T. Newsome, M. N. Shadlen, S. Celebrini and J. A. Movshon (1996). "A relationship between behavioral choice and the visual responses of neurons in macaque MT." Vis Neurosci **13**(1): 87-100.

Bullock, D., P. Cisek and S. Grossberg (1994). "A neural model of voluntary movement and proprioception." Society for Neuroscience Abstracts **20**: 1405.

Burton, A. C., K. Nakamura and M. R. Roesch (2015). "From ventral-medial to dorsal-lateral striatum: neural correlates of reward-guided decision-making." Neurobiol Learn Mem **117**: 51-59.

Busemeyer, J. R. and J. T. Townsend (1993). "Decision field theory: a dynamic-cognitive approach to decision making in an uncertain environment." Psychol.Rev. **100**(3): 432-459.

Carland, M. A., E. Marcos, D. Thura and P. Cisek (2016). "Evidence against perfect integration of sensory information during perceptual decision making." J Neurophysiol **115**(2): 915-930.

Carland, M. A., D. Thura and P. Cisek (2019). "The Urge to Decide and Act: Implications for Brain Function and Dysfunction." Neuroscientist: 1-21.

Chapman, C. S., J. P. Gallivan, D. K. Wood, J. L. Milne, J. C. Culham and M. A. Goodale (2010). "Reaching for the unknown: multiple target encoding and real-time decision-making in a rapid reach task." Cognition **116**(2): 168-176.

Christopoulos, V. N., J. Bonaiuto, I. Kagan and R. A. Andersen (2015). "Inactivation of Parietal Reach Region Affects Reaching But Not Saccade Choices in Internally Guided Decisions." J Neurosci **35**(33): 11719-11728.

Christopoulos, V. N., I. Kagan and R. A. Andersen (2018). "Lateral intraparietal area (LIP) is largely effector-specific in free-choice decisions." Sci Rep **8**(1): 8611.

Cisek, P. (2006). "Integrated neural processes for defining potential actions and deciding between them: A computational model." Journal of Neuroscience **26**(38): 9761-9770.

Cisek, P. (2007). "Cortical mechanisms of action selection: the affordance competition hypothesis." Philosophical Transactions of the Royal Society B: Biological Sciences **362**(1485): 1585-1599.

Cisek, P. (2007). "Cortical mechanisms of action selection: the affordance competition hypothesis." Philos.Trans.R.Soc.Lond B Biol.Sci. **362**(1485): 1585-1599.

Cisek, P. and J. F. Kalaska (2005). "Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action." Neuron **45**(5): 801-814.

Cisek, P. and J. F. Kalaska (2005). "Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action." Neuron **45**(5): 801-814.

Cisek, P. and J. F. Kalaska (2010). "Neural mechanisms for interacting with a world full of action choices." Annu.Rev Neurosci **33**: 269-298.

Cisek, P. and J. F. Kalaska (2010). "Neural mechanisms for interacting with a world full of action choices." Annu Rev Neurosci **33**: 269-298.

Cisek, P. and A. Pastor-Bernier (2014). "On the challenges and mechanisms of embodied decision-making." Philosophical Transactions of the Royal Society B: Biological Sciences **369**.

Cisek, P., G. A. Puskas and S. El-Murr (2009). "Decisions in changing conditions: The urgency-gating model." Journal of Neuroscience **29**(37): 11560-11571.

Coallier, E. and J. F. Kalaska (2014). "Reach target selection in humans using ambiguous decision cues containing variable amounts of conflicting sensory evidence supporting each target choice." J Neurophysiol **112**(11): 2916-2938.

Coallier, E., T. Michelet and J. F. Kalaska (2015). "Dorsal premotor cortex: neural correlates of reach target decisions based on a color-location matching rule and conflicting sensory evidence." J Neurophysiol **113**(10): 3543-3573.

Cos, I., N. Belanger and P. Cisek (2011). "The influence of predicted arm biomechanics on decision-making." J Neurophysiol **105**(6): 3022-3033.

Cos, I., N. Bélanger and P. Cisek (2011). "The influence of predicted arm biomechanics on decision making." Journal of neurophysiology **105**(6): 3022-3033.

Cos, I., J. Duque and P. Cisek (2014). "Rapid prediction of biomechanical costs during action decisions." J Neurophysiol **112**(6): 1256-1266.

Cos, I., F. Medleg and P. Cisek (2012). "The modulatory influence of end-point controllability on decisions between actions." J Neurophysiol **108**(6): 1764-1780.

Cos, I., F. Medleg and P. Cisek (2012). "The modulatory influence of end-point controllability on decisions between actions." J Neurophysiol **108**(6): 1764-1780.

Crammond, D. J. and J. F. Kalaska (2000). "Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity." Journal of Neurophysiology **84**(2): 986-1005.

Croxson, P. L., M. E. Walton, J. X. O'Reilly, T. E. Behrens and M. F. Rushworth (2009). "Effort-based cost-benefit valuation and the human brain." J Neurosci **29**(14): 4531-4541.

Cui, H. and R. A. Andersen (2007). "Posterior parietal cortex encodes autonomously selected motor plans." Neuron **56**(3): 552-559.

d'Avella, A. and E. Bizzi (2005). "Shared and specific muscle synergies in natural motor behaviors." Proc.Natl.Acad.Sci.U.S.A **102**(8): 3076-3081.

d'Avella, A. and E. Bizzi (2005). "Shared and specific muscle synergies in natural motor behaviors." Proc Natl Acad Sci U S A **102**(8): 3076-3081.

Danion, F. R. and J. R. Flanagan (2018). "Different gaze strategies during eye versus hand tracking of a moving target." Scientific Reports **8**.

De Martino, B., D. Kumaran, B. Holt and R. J. Dolan (2009). "The neurobiology of reference-dependent value computation." J Neurosci **29**(12): 3833-3842.

Diamond, J. S., D. M. Wolpert and J. R. Flanagan (2017). "Rapid target foraging with reach or gaze: The hand looks further ahead than the eye." Plos Computational Biology **13**(7).

Ditterich, J., M. E. Mazurek and M. N. Shadlen (2003). "Microstimulation of visual cortex affects the speed of perceptual decisions." Nature Neuroscience **6**(8): 891-898.

Domkin, D., J. Laczko, S. Jaric, H. Johansson and M. L. Latash (2002). "Structure of joint variability in bimanual pointing tasks." Experimental Brain Research **143**(1): 11-23.

Domkin, D., J. Laczko, S. Jaric, H. Johansson and M. L. Latash (2002). "Structure of joint variability in bimanual pointing tasks." Exp Brain Res **143**(1): 11-23.

Drew, T. and D. S. Marigold (2015). "Taking the next step: cortical contributions to the control of locomotion." Curr Opin Neurobiol **33**: 25-33.

Engel, A. K., A. Maye, M. Kurthen and P. Konig (2013). "Where's the action? The pragmatic turn in cognitive science." Trends in Cognitive Sciences **17**(5): 202-209.

Engel, K. C. and J. F. Soechting (2000). "Manual tracking in two dimensions." J Neurophysiol **83**(6): 3483-3496.

Erlhagen, W. and G. Schoner (2002). "Dynamic field theory of movement preparation." Psychol.Rev. **109**(3): 545-572.

Farmer, T. A., S. A. Cargill and M. J. Spivey (2007). "Gradiency and Visual Context in Syntactic Garden-Paths." J Mem.Lang **57**(4): 570-595.

FitzGerald, T. H., B. Seymour and R. J. Dolan (2009). "The role of human orbitofrontal cortex in value comparison for incommensurable objects." J Neurosci **29**(26): 8388-8395.

Fitzpatrick, R. C. and B. L. Day (2004). "Probing the human vestibular system with galvanic stimulation." J Appl Physiol (1985) **96**(6): 2301-2316.

Floresco, S. B. (2015). "The nucleus accumbens: an interface between cognition, emotion, and action." Annu Rev Psychol **66**: 25-52.

Forstmann, B. U., S. Brown, G. Dutilh, J. Neumann and E.-J. Wagenmakers (2010). "The neural substrate of prior information in perceptual decision making: a model-based analysis." Frontiers in human neuroscience **4**: 40.

Forstmann, B. U., G. Dutilh, S. Brown, J. Neumann, D. Y. Von Cramon, K. R. Ridderinkhof and E.-J. Wagenmakers (2008). "Striatum and pre-SMA facilitate decision-making under time pressure." Proceedings of the National Academy of Sciences **105**(45): 17538-17542.

Gallivan, J. P., C. S. Chapman, D. M. Wolpert and J. R. Flanagan (2018). "Decision-making in sensorimotor control." Nat Rev Neurosci **19**(9): 519-534.

Gallivan, J. P., C. S. Chapman, D. K. Wood, J. L. Milne, D. Ansari, J. C. Culham and M. A. Goodale (2011). "One to four, and nothing more: nonconscious parallel individuation of objects during action planning." Psychol.Sci. **22**(6): 803-811.

Gallivan, J. P., L. Logan, D. M. Wolpert and J. R. Flanagan (2016). "Parallel specification of competing sensorimotor control policies for alternative action options." Nat Neurosci **19**(2): 320-326.

Gibson, J. J. (1979). The ecological approach to visual perception. Boston, Houghton Mifflin.

Gold, J. I. and M. N. Shadlen (2000). "Representation of a perceptual decision in developing oculomotor commands." Nature **404**(6776): 390-394.

Gold, J. I. and M. N. Shadlen (2000). "Representation of a perceptual decision in developing oculomotor commands." Nature **404**(6776): 390-394.

Gold, J. I. and M. N. Shadlen (2007). "The neural basis of decision making." Annu Rev Neurosci **30**: 535-574.

Gold, J. I. and M. N. Shadlen (2007). "The neural basis of decision making." Annu.Rev.Neurosci. **30**: 535-574.

Gregorios-Pippas, L., P. N. Tobler and W. Schultz (2009). "Short-term temporal discounting of reward value in human ventral striatum." J Neurophysiol **101**(3): 1507-1523.

Grossberg, S. (1973). "Contour enhancement, short term memory, and constancies in reverberating neural networks." Studies in Applied Mathematics **52**: 213-257.

Haith, A. M., D. M. Huberdeau and J. W. Krakauer (2015). "Hedging your bets: intermediate movements as optimal behavior in the context of an incomplete decision." PLoS Comput Biol **11**(3): e1004171.

Hanes, D. P. and J. D. Schall (1996). "Neural control of voluntary movement initiation." Science **274**: 427-430.

Hernandez, A., A. Zainos and R. Romo (2000). "Neuronal correlates of sensory discrimination in the somatosensory cortex." Proc Natl Acad Sci U S A **97**(11): 6191-6196.

Horwitz, G. D. and W. T. Newsome (1999). "Separate signals for target selection and movement specification in the superior colliculus." Science **284**(5417): 1158-1161.

Horwitz, G. D. and W. T. Newsome (2001). "Target selection for saccadic eye movements: prelude activity in the superior colliculus during a direction-discrimination task." J Neurophysiol **86**(5): 2543-2558.

Huk, A. C. and M. N. Shadlen (2005). "Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making." Journal of Neuroscience **25**(45): 10420-10436.

Johnson, P. B., S. Ferraina, L. Bianchi and R. Caminiti (1996). "Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal arm regions." Cerebral Cortex **6**(2): 102-119.

Jones, E. G., J. D. Coulter and H. C. Hendry (1978). "Intracortical connectivity of achitectonic fields in the somatic sensory, motor and parietal cortex of monkeys." Journal of Comparative Neurology **181**: 291-348.

Kable, J. W. and P. W. Glimcher (2007). "The neural correlates of subjective value during intertemporal choice." Nat Neurosci **10**(12): 1625-1633.

Kalaska, J. F., D. A. Cohen, M. L. Hyde and M. Prud'homme (1989). "A comparison of movement direction-related versus load direction- related activity in primate motor cortex, using a two-dimensional reaching task." The Journal of Neuroscience **9**(6): 2080-2102.

Kalaska, J. F., D. A. D. Cohen, M. L. Hyde and M. J. Prud'homme (1989). "A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task." Journal of Neuroscience **9**(6): 2080-2102.

Kalaska, J. F. and D. J. Crammond (1995). "Deciding not to GO: Neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex." Cerebral Cortex **5**: 410-428.

Kalenscher, T., P. N. Tobler, W. Huijbers, S. M. Daselaar and C. M. Pennartz (2010). "Neural signatures of intransitive preferences." Front Hum Neurosci **4**.

Kaufman, M. T., M. M. Churchland, S. I. Ryu and K. V. Shenoy (2014). "Cortical activity in the null space: permitting preparation without movement." Nat Neurosci **17**(3): 440-448.

Kennerley, S. W., T. E. Behrens and J. D. Wallis (2011). "Double dissociation of value computations in orbitofrontal and anterior cingulate neurons." Nat Neurosci **14**(12): 1581-1589.

Keyser, J., W. P. Medendorp and L. P. J. Selen (2017). "Task-dependent vestibular feedback responses in reaching." J Neurophysiol **118**(1): 84-92.

Kim, S., J. Hwang and D. Lee (2008). "Prefrontal coding of temporally discounted values during intertemporal choice." Neuron **59**(1): 161-172.

Klaes, C., S. Schneegans, G. Schoner and A. Gail (2012). "Sensorimotor learning biases choice behavior: a learning neural field model for decision making." PLoS Comput Biol **8**(11): e1002774.

Klaes, C., S. Westendorff, S. Chakrabarti and A. Gail (2011). "Choosing goals, not rules: deciding among rule-based action plans." Neuron **70**(3): 536-548.

Klein-Flugge, M. C. and S. Bestmann (2012). "Time-dependent changes in human corticospinal excitability reveal value-based competition for action during decision processing." J Neurosci **32**(24): 8373-8382.

Laming, D. (1968). Information theory of choice reaction time. New York, Wiley.

Lepora, N. F. and G. Pezzulo (2015). "Embodied choice: how action influences perceptual decision making." PLoS Comput Biol **11**(4): e1004110.

Levy, D. J. and P. W. Glimcher (2012). "The root of all value: a neural common currency for choice." Current Opinion in Neurobiology **22**(6): 1027-1038.

Marcos, E., I. Cos, B. Girard and P. F. Verschure (2015). "Motor Cost Influences Perceptual Decisions." PLoS One **10**(12): e0144841.

Mather, J. A. and C. Putchat (1983). "Parallel Ocular and Manual Tracking Responses to a Continuously Moving Visual Target." Journal of Motor Behavior **15**(1): 29-38.

Mazurek, M. E., J. D. Roitman, J. Ditterich and M. N. Shadlen (2003). "A role for neural integrators in perceptual decision making." Cerebral Cortex **13**(11): 1257-1269.

McKinstry, C., R. Dale and M. J. Spivey (2008). "Action dynamics reveal parallel competition in decision making." Psychol.Sci. **19**(1): 22-24.

McPeek, R. M. and E. L. Keller (2002). "Superior colliculus activity related to concurrent processing of saccade goals in a visual search task." Journal of Neurophysiology **87**(4): 1805-1815.

Miall, R. C., D. J. Weir and J. F. Stein (1993). "Intermittency in human manual tracking tasks." J Mot Behav **25**(1): 53-63.

Michalski, J. and P. Cisek (2017). "Deciding while acting – an investigation of decision-making during ongoing action control." Society for Neuroscience Abstracts.

Michalski, J., A. M. Green and P. Cisek (2018). "An investigation of reach decision preferences during ongoing action control." Society for Neuroscience Abstracts.

Moreau-Debord, I., C. Z. Martin, M. Landry and A. M. Green (2014). "Evidence for a reference frame transformation of vestibular signal contributions to voluntary reaching." J Neurophysiol **111**(9): 1903-1919.

Morel, P., P. Ulbrich and A. Gail (2017). "What makes a reach movement effortful? Physical effort discounting supports common minimization principles in decision making and motor control." PLoS Biol **15**(6): e2001323.

Mulder, M. J., M. C. Keuken, L. van Maanen, W. Boekel, B. U. Forstmann and E. J. Wagenmakers (2013). "The speed and accuracy of perceptual decisions in a random-tone pitch task." Atten Percept Psychophys **75**(5): 1048-1058.

Nakajima, T., N. Fortier-Lebel and T. Drew (2019). "Premotor Cortex Provides a Substrate for the Temporal Transformation of Information During the Planning of Gait Modifications." Cereb Cortex.

Nashed, J. Y., F. Crevecoeur and S. H. Scott (2012). "Influence of the behavioral goal and environmental obstacles on rapid feedback responses." J Neurophysiol **108**(4): 999-1009.

Nashed, J. Y., F. Crevecoeur and S. H. Scott (2014). "Rapid online selection between multiple motor plans." Journal of Neuroscience **34**(5): 1769-1780.

Nashed, J. Y., F. Crevecoeur and S. H. Scott (2014). "Rapid online selection between multiple motor plans." J Neurosci **34**(5): 1769-1780.

Nikolova, G. S. and Y. E. Toshev (2007). "Estimation of male and female body segment parameters of the Bulgarian population using a 16-segmental mathematical model." Journal of Biomechanics **40**(16): 3700-3707.

Noonan, M. P., M. E. Walton, T. E. Behrens, J. Sallet, M. J. Buckley and M. F. Rushworth (2010). "Separate value comparison and learning mechanisms in macaque medial and lateral orbitofrontal cortex." Proc Natl Acad Sci U S A **107**(47): 20547-20552.

Padoa-Schioppa, C. (2011). "Neurobiology of economic choice: a good-based model." Annu.Rev Neurosci **34**: 333-359.

Padoa-Schioppa, C. and J. A. Assad (2006). "Neurons in the orbitofrontal cortex encode economic value." Nature **441**(7090): 223-226.

Palmer, J., A. C. Huk and M. N. Shadlen (2005). "The effect of stimulus strength on the speed and accuracy of a perceptual decision." J Vis **5**(5): 376-404.

Pandya, D. N. and E. H. Yeterian (1985). Architecture and connections of cortical association areas. Cerebral Cortex. A. Peters and E. G. Jones. New York, Plenum. **4:** 3-61.

Parker, A. J. and W. T. Newsome (1998). "Sense and the single neuron: probing the physiology of perception." Annu Rev Neurosci **21**: 227-277.

Pasalar, S., A. V. Roitman, W. K. Durfee and T. J. Ebner (2006). "Force field effects on cerebellar Purkinje cell discharge with implications for internal models." Nature Neuroscience **9**(11): 1404-1411.

Pasquereau, B. and R. S. Turner (2013). "Limited encoding of effort by dopamine neurons in a cost-benefit trade-off task." J Neurosci **33**(19): 8288-8300.

Pastor-Bernier, A. and P. Cisek (2011). "Neural correlates of biased competition in premotor cortex." J Neurosci **31**(19): 7083-7088.

Peixoto, D., R. Kiani, C. Chandrasekaran, S. I. Ryu, K. V. Shenoy and W. T. Newsome (2018). "Population dynamics of choice representation in dorsal premotor and primary motor cortex." BioRxiv: 283960.

Pesaran, B., M. J. Nelson and R. A. Andersen (2008). "Free choice activates a decision circuit between frontal and parietal cortex." Nature **453**(7193): 406-409.

Peters, J. and C. Buchel (2009). "Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making." J Neurosci **29**(50): 15727-15734.

Pezzulo, G. and C. Castelfranchi (2009). "Thinking as the control of imagination: a conceptual framework for goal-directed systems." Psychol.Res. **73**(4): 559-577.

Pezzulo, G. and P. Cisek (2016). "Navigating the Affordance Landscape: Feedback Control as a Process Model of Behavior and Cognition." Trends Cogn Sci **20**(6): 414-424.

Plassmann, H., J. O'Doherty and A. Rangel (2007). "Orbitofrontal cortex encodes willingness to pay in everyday economic transactions." J Neurosci **27**(37): 9984-9988.

Platt, M. L. and P. W. Glimcher (1999). "Neural correlates of decision variables in parietal cortex." Nature **400**(6741): 233-238.

Platt, M. L. and P. W. Glimcher (1999). "Neural correlates of decision variables in parietal cortex." Nature **400**(6741): 233-238.

Pruszynski, J. A., I. Kurtzer, J. Y. Nashed, M. Omrani, B. Brouwer and S. H. Scott (2011). "Primary motor cortex underlies multi-joint integration for fast feedback control." Nature **478**(7369): 387-390.

Rangel, A., C. Camerer and P. R. Montague (2008). "A framework for studying the neurobiology of value-based decision making." Nat Rev Neurosci **9**(7): 545-556.

Ratcliff, R. (1978). "A theory of memory retrieval." Psychological review **85**: 59-78.

Ratcliff, R. (1978). "A theory of memory retrieval." Psychological Review **83**: 59-108.

Ratcliff, R. and G. McKoon (2008). "The diffusion decision model: theory and data for two-choice decision tasks." Neural Comput **20**(4): 873-922.

Ratcliff, R. and J. N. Rouder (1998). "Modeling response times for two-choice decisions." Psychological science **9**(5): 347-356.

Roitman, J. D. and M. N. Shadlen (2002). "Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task." J Neurosci **22**(21): 9475-9489.

Roitman, J. D. and M. N. Shadlen (2002). "Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task." Journal of Neuroscience **22**(21): 9475-9489.

Sato, N., H. Sakata, Y. L. Tanaka and M. Taira (2006). "Navigation-associated medial parietal neurons in monkeys." Proc Natl Acad Sci U S A **103**(45): 17001-17006.

Sato, N., H. Sakata, Y. L. Tanaka and M. Taira (2010). "Context-dependent place-selective responses of the neurons in the medial parietal region of macaque monkeys." Cereb Cortex **20**(4): 846-858.

Scherberger, H. and R. A. Andersen (2007). "Target selection signals for arm reaching in the posterior parietal cortex." Journal of Neuroscience **27**(8): 2001-2012.

Selen, L. P., M. N. Shadlen and D. M. Wolpert (2012). "Deliberation in the motor system: reflex gains track evolving evidence leading to a decision." J Neurosci **32**(7): 2276-2286.

Shadlen, M. N., K. H. Britten, W. T. Newsome and J. A. Movshon (1996). "A computational analysis of the relationship between neuronal and behavioral responses to visual motion." The Journal of Neuroscience **16**(4): 1486-1510.

Shadmehr, R., H. J. Huang and A. A. Ahmed (2016). "A Representation of Effort in Decision-Making and Motor Control." Curr Biol **26**(14): 1929-1934.

Shafir, S., T. Waite and B. Smith (2002). "Context-dependent violations of rational choice in honeybees (Apis mellifera) and gray jays (Perisoreus canadensis)." Behavioral Ecology and Sociobiology **51**(2): 180-187.

Smith, P. L. and R. Ratcliff (2004). "Psychology and neurobiology of simple decisions." Trends Neurosci **27**(3): 161-168.

Song, J. H. and K. Nakayama (2008). "Target selection in visual search as revealed by movement trajectories." Vision Research **48**(7): 853-861.

Song, J. H. and K. Nakayama (2009). "Hidden cognitive states revealed in choice reaching tasks." Trends Cogn Sci. **13**(8): 360-366.

Stone, M. (1960). "Models for choice reaction time." Psychometrika **25**: 251-260.

Takarada, Y., T. Mima, M. Abe, M. Nakatsuka and M. Taira (2014). "Inhibition of the primary motor cortex can alter one's "sense of effort": effects of low-frequency rTMS." Neurosci Res **89**: 54-60.

Thompson, K. G., D. P. Hanes, N. P. Bichot and J. D. Schall (1996). "Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search." J Neurophysiol **76**(6): 4040-4055.

Thura, D., J. Beauregard-Racine, C. W. Fradet and P. Cisek (2012). "Decision making by urgency gating: theory and experimental support." J Neurophysiol **108**(11): 2912-2930.

Thura, D. and P. Cisek (2014). "Deliberation and commitment in the premotor and primary motor cortex during dynamic decision making." Neuron **81**(6): 1401-1416.

Tresch, M. C. and A. Jarc (2009). "The case for and against muscle synergies." Curr Opin Neurobiol **19**(6): 601-607.

Tversky, A. (1969). "Intransitivity of preferences." Psychological Review **76**(1): 31-48.

Usher, M. and J. L. McClelland (2001). "The time course of perceptual choice: the leaky, competing accumulator model." Psychol.Rev. **108**(3): 550-592.

van Elswijk, G., B. U. Kleine, S. Overeem and D. F. Stegeman (2007). "Expectancy induces dynamic modulation of corticospinal excitability." J Cogn Neurosci **19**(1): 121-131.

van Veen, V., M. K. Krug and C. S. Carter (2008). "The neural and computational basis of controlled speed-accuracy tradeoff during task performance." J Cogn Neurosci **20**(11): 1952-1965.

Vandekerckhove, J., F. Tuerlinckx and M. D. Lee (2011). "Hierarchical diffusion models for two-choice response times." Psychological methods **16**(1): 44.

Wagenmakers, E. J., R. Ratcliff, P. Gomez and G. McKoon (2008). "A Diffusion Model Account of Criterion Shifts in the Lexical Decision Task." J Mem Lang **58**(1): 140-159.

Walton, M. E., D. M. Bannerman, K. Alterescu and M. F. S. Rushworth (2003). "Functional Specialization within Medial Frontal Cortex of the Anterior Cingulate for Evaluating Effort-Related Decisions." The Journal of Neuroscience **23**(16): 6475-6479.

Wang, X. J. (2002). "Probabilistic decision making by slow reverberation in cortical circuits." Neuron **36**(5): 955-968.

Westendorff, S., C. Klaes and A. Gail (2010). "The cortical timeline for deciding on reach motor goals." J Neurosci **30**(15): 5426-5436.

Wise, S. P., D. Boussaoud, P. B. Johnson and R. Caminiti (1997). "Premotor and parietal cortex: corticocortical connectivity and combinatorial computations." Annu.Rev.Neurosci. **20**: 25-42.

Wood, D. K., J. P. Gallivan, C. S. Chapman, J. L. Milne, J. C. Culham and M. A. Goodale (2011). "Visual salience dominates early visuomotor competition in reaching behavior." J Vis. **11**(10).

Yoon, T., R. B. Geary, A. A. Ahmed and R. Shadmehr (2018). "Control of movement vigor and decision making during foraging." Proc Natl Acad Sci U S A **115**(44): E10476-E10485.