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Cox, Ralf F.A.

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A Dynamic Model of Human Limb Selection

Ralf F. A. Cox 

Department of Psychology, University of Groningen, 9712 TS Groningen, The Netherlands; r.f.a.cox@rug.nl

Abstract: Two experiments and a dynamic model for human limb selection are reported. In Experiment 1, left-handed and right-handed participants ($N = 36$) repeatedly used one hand for grasping a small cube. After a clear switch in the cube's location, perseverative limb selection was revealed in both handedness groups. In Experiment 2, the cubes were presented in a clockwise and counter-clockwise sequence to right-handed participants ($N = 15$). A spatial shift in the switch point between right-hand use and left-hand use was observed. The model simulates the experiments by implementing the nonlinear multiple-timescale dynamics of the action-selection process underlying limb selection. It integrates two mechanisms that were earlier proposed to underlie this selection aspect of manual activity: limb dominance and attentional information. Finally, the model is used to simulate an influential earlier experiment, by establishing a conceptual link between cross-lateral inhibition asymmetry and the direction and strength of handedness.

Keywords: action selection; handedness; dynamic model; perseveration; hysteresis

1. Introduction

Choices about which (bodily) means to use to reach a certain goal constitute an integral part of action planning in any type of daily activity, from selecting the right tool for a job, to choosing the appropriate hand for grasping a coffee mug. In general, planning in goal-directed behavior entails choices about goals, means, and the specifics of how to couple and sequence those goals and means. The present study addresses the action planning in limb selection, more specifically, the action-selection process underlying the choice of which hand to use as a means in performing a unimanual grasping task. The options available in such a task are of course discrete; either the right hand or the left hand, making it a binary system. One important factor involved is a person's handedness, but cultural, habitual, and perceptual factors, as well as task complexity, contribute too [1–8], which makes it particularly interesting as a case study for planning. Moreover, depending on the task and context, these factors can be reinforcing or competing in their contribution to the choice, temporarily favoring one hand above the other. This is evidently true for everyone who has ever experienced the difficulty of retrieving one's keys out of one's trouser pocket while holding a large bag of groceries in each hand.

As mentioned, an important controlling factor for limb selection in a unimanual task is handedness. Handedness is often considered an invariant trait that determines a person's hand use in a large number of tasks (for an overview on handedness see [9–11]). A more contemporary view, which I will adopt here, takes other factors (i.e., from the environment and the task) into account, conceiving handedness, both in its direction and strength, as merely an internal predisposition or tendency to favor one hand above the other, not as the sole determinant in limb selection. This tendency can be counteracted when external stimulation becomes laterally specified or more demanding on the action system, as, for example, in grasping a tool in hemispace. This view is motivated by the observation that it is virtually meaningless to talk about a person's dominant limb without doing a thorough analysis of the task with which it is measured. Handedness is neither a fixed nor a static biological trait, but is highly dependent on many contextual aspects of the task. Note that



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from this perspective, it seems reasonable to think of handedness in terms of a likelihood function for using one or the other hand.

As a general framework, one can roughly classify the relevant factors in limb selection into three categories of constraints, according to their relation to the action system: organismic, environmental, and task constraints [12–14]. Each of these constraints does not serve as a single cause of behavior, but rather as a limiting factor on the action possibilities that are available for an organism (actor). The organismic constraints are best viewed as internal to the actor's action system. It means that the actor is subjected to constraints resulting from the specific biomechanics and neuroanatomy of his or her body, but also from the history of prior actions, as far as they altered the state of the action system in any way. Environmental constraints and task constraints are external to the actor's action system, and entail perceptual information with respect to the environment and the task. These constraints are placed upon the actor by the environment, in which the activities are embedded, and the nature and specifics of the task at hand (i.e., its goals, the available means, but also rules, conventions, and culture). Note that the distinction between environmental constraints and task constraint is not very strict. It depends on the actor's freedom of manipulating these constraints. Note also that, in addition to their relation to the action system, another relevant and differentiating aspect of these action constraints is the timescale on which they are exerting their influence. This aspect will prove to be fundamental for our account of limb selection, and I will elaborate on it shortly.

How do the different constraints coalesce in the planning? And how does limb selection come about as a result? In order to shed more light on these questions, the following simple but elegant experiment was performed [15]. Adult participants were asked to grasp a small object that was randomly placed at nine different locations in hemispace. The locations varied in laterality from left to right, keeping an equal distance to the body center on a half-circle in front of the participant (see Figure 1). The upper part of Table 1 presents the results of their experiment. The overall response profile can be characterized as a tendency for ipsilateral reaching (i.e., the hand at the same side as the object) in the two hemispace sides, and use of the dominant limb at midline. This means that participants used their nonpreferred hand when the object was presented on their nonpreferred side. Although this general pattern was similar for both laterality groups, right-handers demonstrated a stronger preference for their dominant limb compared to left-handers. This can be gathered from the larger deviations from ipsilateral reaching at the nonpreferred side in this group (see Table 1). Others reported comparable findings in adults [16–19], and also in children [11,19,20].

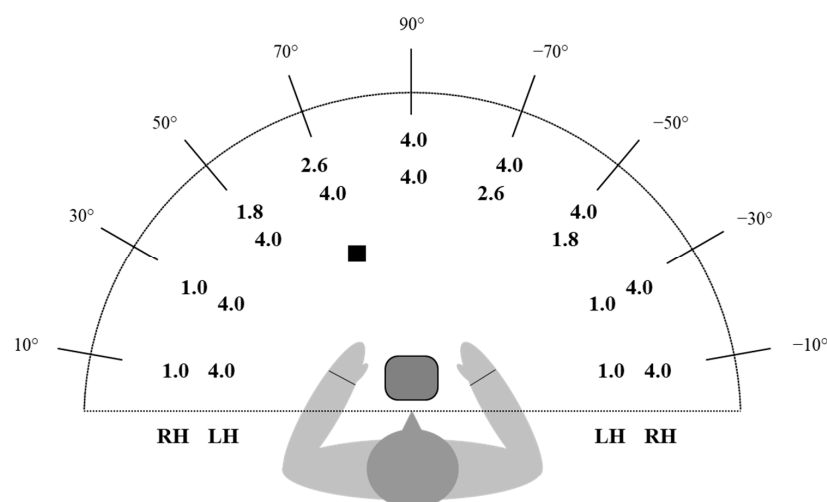


Figure 1. Setup of Gabbard et al.'s (1997) [15] experiment. The small black square represents the 1-inch³ cube which the participant had to grasp at every trial, and the dark-grey rectangle represents the box they had to put them in. The numbers indicate the strength of the perceptual input for the left hand (LH) and right hand (RH) for the different object locations as used in the model simulations.

Table 1. Results of Gabbard et al. (1997) [15] and of our model simulating this experiment: proportion of preferred-hand use for the nine (randomly presented) object positions. Inspired by these results, two mechanisms underlying limb selection were hypothesized: limb dominance and attentional information [21,22]. As stated by the authors, limb dominance, or handedness as it is often referred to, is largely responsible for the hand choice in the ipsilateral hemisphere and on midline. In terms of categories of constraints [12], this mechanism belongs to the organismic constraints, as it is related to an asymmetry of the organism, be it functional or possibly even structural. Attentional information is supposed to be responsible for altering the hand choice in the contralateral hemisphere. The nature of the attentional information is conceived to be perceptual [21,22], and its composition is determined by the spatial layout of the relevant objects in the task. Depending on the specifics of the task, it either fits into the category of environmental constraints or task constraints [12], as it is external to the organism's action system.

Group	Left Hemisphere				Right Hemisphere				
	10°	30°	50°	70°	90°	−70°	−50°	−30°	−10°
Empirical results									
Left-handers (N = 60)	0.98	0.98	0.98	0.93	0.75	0.30	0.13	0.07	0.08
Right-handers (N = 84)	0.20	0.19	0.25	0.42	0.95	0.99	0.99	1.00	1.00
Simulation results (N = 500)									
Left-handers	1.00	1.00	1.00	0.98	0.78	0.30	0.10	0.04	0.03
Right-handers	0.13	0.09	0.24	0.51	0.93	1.00	1.00	1.00	1.00

Despite the obvious relevance of these mechanisms and the ample empirical evidence that stresses the multicausality of limb selection, we still lack a general framework for integrating these ideas in a concise explanation of how the choice to use a particular hand comes about. Put differently, as to date, there is no working model for limb selection that can reproduce the empirical findings. As a minor point, the mechanisms do not offer an (testable) explanation for the differences in laterality strength between left-handers and right-handers.

The goal of this paper is two-fold. First, adding to the empirical realm and theoretical discussion on limb selection, the aspect of multiple-timescale dynamics. To investigate this, experiments were performed in which the sequence of earlier limb selections was manipulated, thereby varying its possible effects on subsequent selections. Second, introducing a working dynamical model for the action-selection process underlying limb selection, which integrates and extends the earlier proposed mechanisms [21,22]. In this way, these mechanisms are treated in accordance with the idea of constraints on action selection [12], rather than as single-cause all-or-none explanations of this kind of behavior. I will show that the model reproduces the results of the reported experiments, and the original experiment [15].

I report two experiments. In both experiments, adult participants who were sitting at a table had to pick up a small cube on each trial, and displace it to a box in front of them. In Experiment 1, participants received a series of trials in which the cubes were first placed at lateral positions, either four times on the extreme left side or four times on the extreme right side. This constituted a series of training trials, building a memory trace (i.e., a short-term bias) for using one particular hand. To measure the possible effect of this memory trace on subsequent hand choices, this set of training trials was followed by two more trials in which the object was presented on the participant's midline. For each participant, a set of training trials was offered to the preferred hand and nonpreferred hand, in two separate conditions. In Experiment 2, right-handed participants received a clockwise and counter-clockwise sequence of cube presentations on the nine different positions in the original task [15]. Each participant received both sequences in two separate conditions. The main objective in this experiment was to detect differences in the pattern of hand use across hemisphere as a function of the type of sequence that has been performed.

In light of the earlier results [15] and the expected effect of earlier limb selections on upcoming ones, I formulated two major hypotheses with respect to Experiment 1. First, I expected an increase in the number of nonpreferred-hand uses at midline after a set of

training trials at the nonpreferred hand. This effect is what will be called perseverative limb selection, resulting from a short-term bias built up during the training set. Only a small increase in the number of preferred-hand uses was expected after the training series for the preferred hand, due to a ceiling effect. Second, because of the difference in handedness strength between the two laterality groups, I expected to find a difference in the size of the perseveration effect. Left-handers were hypothesized to demonstrate a stronger effect of perseveration, because they already switch more easily to their nonpreferred hand. Therefore, the effect of the short-term bias on future choices was reasoned to stand a better 'chance' in the process next to the weaker (compared to right-handers) long-term bias of the hand preference.

In Experiment 2, when presenting the cubes in a clockwise sequence, I expected to see a (spatial) delay in the location of the switch from grasping the cube with the left hand to grasping it with the right hand (compared to a random task [15]). This is the well-known hysteresis effect, which is amongst the basic 'flags' of nonlinear behavior in dynamical systems. Examples of hysteresis in human behavior are numerous [23–28]. It has not been studied explicitly in limb selection though, except for switching between unimanual and bimanual reaching and grasping [29–31]. In one study participants performed a sequence of the same unimanual action, starting from the body midline and extending to the left or right [32]. At some point, a transition occurred from using one hand to using the other. Because the task was performed in only one direction, a possible divergence of the transition point could not be considered. The same hysteresis effect was expected for right-hand grasping switching into left-hand grasping in a counter-clockwise sequence.

2. Experiment 1

2.1. Method

Participants. Twenty strongly left-handed adults (5 male and 15 female) and 24 strongly right-handed adults (4 male and 20 female). The direction and strength of the hand-preference was assessed using the four items of the manual part of the Lateral Preference Inventory for measurement of handedness, footedness, eyedness, and earedness [33]. As was expected, it was more difficult to find strongly left-handers (i.e., with four consistent left-hand answers on the inventory) than strongly right-handers. The mean age of the participants was 21.8 years (range: 19–28 years). None of the participants had a visual or physical impairment that could interfere with task performance. In particular, they all had normal or corrected to normal eyesight. The study was conducted in accordance with the Declaration of Helsinki, and all participants gave their informed consent.

Procedure. Participants were seated on a chair in front of a table (75 cm × 150 cm × 75 cm high), with an experimenter facing them on the opposite side. On this table, nine locations were marked on a half-circle, with the participant at its center, at slightly less than an arm length away. These locations were set at 20 degrees intervals, starting at 10 degrees relative to the edge of the table. This composed the following series: 10°, 30°, 50°, and 70° on the left side of the participant, 90° (equaling the participant's midline), and –70°, –50°, –30°, and –10° on the right side of the participant (see Figure 1). In the following, the minus sign will be used to denote locations in the right hemisphere.

A 1-inch³ cube was placed at one of these locations on each trial. Participants were asked to grasp the cube with one hand and transport it to a small box in front of them. Before the start of each trial, participants were instructed to close their eyes while the experimenter positioned the cube. After a verbal signal ("OK") from the experimenter, the participant opened their eyes and reached for the object. It was made clear that there was no need for a speedy reaction, but that enough time could be taken to make a decision to use one of the hands. Participants were unaware of the goal of the experiment.

The experiment consisted of three conditions. Two conditions started by establishing a short-term bias for one of the hands, by offering a set of four training trials: T₁, T₂, T₃, and T₄. In one of the conditions, the participant's left hand was trained, and in the other condition the participant's right hand. Note that this means that each participant was

trained on the preferred hand (PHC), as well as on the nonpreferred hand (NPHC). In the training trials, the cube was presented successively at the 10° , 30° , 10° , and 30° locations on the left side (left-hand training), or at the -10° , -30° , -10° , and -30° locations on the right side (right-hand training). Participants were free to choose the hand with which to grasp the cube. In two subsequent 'neutral' trials, N_1 and N_2 , the cube was presented at midline (90°), allowing us to determine the participant's choice of limb on midline after the set of training trials. The order of the two training conditions was counterbalanced.

In between these two training conditions, the original experiment [15] was performed. This third condition was performed in order to establish a baseline proportion of preferred-hand use on midline. The rationale was that a randomized series of hand choices (i.e., no specific bias), with an otherwise similar setup, would provide the most valid estimate for midline performance in this task. This random condition (RC) consisted of a series of nine trials in which the cube was placed on the table in each of the nine locations of Figure 1 in a completely randomized order. Since this condition copied the original procedure [15] as a bonus, this enabled us to replicate their findings.

2.2. Results and Discussion

Random condition. In the random condition, I found a similar pattern of hand use as in the original study [15]. Despite this overall pattern, I found no significant differences between left-handers and right-handers on any of the specific locations. This may be due to a relatively small number of participants, which was about one-third of the original study [15].

Training conditions. The following results include 19 left-handed participants and 17 right-handed participants. The reason for these numbers to be smaller than the total number of participants in each handedness group is that not all participants turned out to be 'trainable' on their nonpreferred hand. In our experimental procedure, I deliberately did not instruct the participants to use the ipsilateral hand in the training trials, because of the obvious possibility of transfer of this instruction to the neutral trials. As a result, a number of participants used their preferred hand rather than their nonpreferred hand when the cubes were presented on their nonpreferred side (i.e., contralateral with respect to cube position), despite the awkward across-midline reaching that this entails. As might be expected from the well-known difference in laterality strength between the handedness groups (although not found here), this number was considerably larger in the group of right-handers (seven participants) than in the group of left-handers (one participant). The participants who were not 'trainable' all used their preferred hand at all six trials in both conditions.

In the following analyses, only the data of the participants who completed all training trials (T_1 to T_4) with the appropriate hand were used, that is, ipsilateral with respect to the object. This constituted a group with a well-established short-term bias for that hand, and for whom perseverative limb selection might be expected. The results of the two training conditions are presented in Table 2. From the replication of the [15] experiment in the random condition, I obtained a baseline proportion of preferred-hand use on midline (90°). This was 0.84 for the left-handers and 0.88 for the right-handers. In the following, I will discuss the main findings of the experiment.

First, the data of the two handedness groups were collapsed and analyzed as a single group of 36 participants. I tested if the proportions of preferred-hand use on midline differed between the two training conditions (PHC and NPHC) and the random condition (RC). This was performed for the first neutral trial (N_1) and the second neutral trial (N_2) separately, using Cochran tests for comparing three related samples. For the N_1 trial, there was a significant difference between PHC, NPHC, and RC, $Q(df = 2, N = 36) = 26.000$, $p < 0.001$. This was also the case for the N_2 trial, $Q(df = 2, N = 36) = 18.000$, $p < 0.001$. These analyses show that, overall, the participants demonstrated a different pattern of limb selection on midline, depending on the sequence of earlier choices that have been

made. This clearly shows that perseveration is present in adult limb selection, at least in unimanual grasping on midline.

Table 2. Results of the training conditions of Experiment 1: proportion of preferred-hand use in the four training trials (T₁–T₄) and the two neutral trials (N₁ and N₂). The proportion of preferred-hand use for the 90° location in the random task (Experiment 1) was 0.84 for the left-handers, and 0.88 for the right-handers.

Group	T ₁ –T ₄	N ₁	N ₂
Left-handers (N = 19)			
Preferred-hand training	1	1	1
Nonpreferred-hand training	0.00	0.53	0.58
Right-handers (N = 17)			
Preferred-hand training	1	0.94	0.88
Nonpreferred-hand training	0.00	0.53	0.65

To analyze these findings more closely, I used McNemar tests for comparing two related samples to test whether the differences in the proportions of preferred-hand use in the combinations PHC–RC, NPHC–RC, and PHC–NPHC were significant. For both trials (N₁ and N₂), there were significant differences in the proportions of preferred-hand use between NPHC and RC ($p < 0.001$, and, $p < 0.001$, respectively), and between PHC and NPHC ($p < 0.01$, and, $p < 0.001$, respectively). After performing a set of training trials with the nonpreferred hand, participants subsequently used this hand more often, compared to performing a set of training trials with the preferred hand, or after having no specific bias at all. This is still true for the subsequent neutral trial (N₂). Taken together, these results confirm the conclusion of perseverative limb selection in adult unimanual grasping.

Next, to study this effect as a function of handedness, I analyzed the results for left-handers and right-handers separately. For both handedness groups, Cochran tests revealed that the proportions of preferred-hand use on midline significantly differed between PHC, NPHC, and RC in both neutral trials (all p 's < 0.01 , except for the N₂ trial for the right-handers, $p < 0.05$).

Finally, McNemar tests revealed that for both handedness groups, the differences in the proportions of preferred-hand use were significant between NPHC and RC ($p < 0.05$, for left-handers and right-handers), and between PHC and NPHC ($p < 0.01$ and $p < 0.05$, for left-handers and right-handers, respectively), for the first neutral trial. For the second neutral trial, only the difference between PHC and NPHC was significant in the left-handed group ($p < 0.01$). Although perseverance was present for both handedness groups in the first neutral trial, these analyses demonstrate a difference in the strength of the effect for the second neutral trial. Right-handers no longer use the nonpreferred hand in the second subsequent trial more often after a specific bias for that hand. In other words, the effect of the earlier limb selections is no longer strong enough to overrule the hand preference.

3. Experiment 2

3.1. Method

Participants. Fifteen strongly right-handed adult volunteers (3 male and 12 female) with a mean age of 21.4 years (range: 19–25 years) participated in the experiment. The study was conducted in accordance with the Declaration of Helsinki, and all participants gave their informed consent.

Procedure. The general procedure was the same as in the previous experiment, and closely followed the original procedure [15]. Experiment 2 consisted of three conditions, each with a series of nine successive cube presentations. Two of them were sequential conditions: a clockwise condition and a counter-clockwise condition. In the clockwise condition, starting with the 10° location on the participant's left side, the experimenter sequentially placed the cube on each following location of Figure 1, up until the –10° location on the participant's right side. In the counter-clockwise condition the experimenter

placed the cube in a similar but opposite fashion, starting on the participant’s right side at the -10° location. The order of the two sequential conditions was counterbalanced. As in Experiment 1, the original experiment [15] was replicated as a third condition in between the two sequential conditions. In this condition, the cube was randomly placed in each of the nine locations of Figure 1.

3.2. Results and Discussion

The results of the two sequential conditions are presented in Table 3. To highlight the effects, the proportions of preferred-hand use for the 50° , 70° , and 90° locations are also shown in Figure 2. Figure 2 also shows the scores of the participants for these trials in the random condition.

Table 3. Results of the sequential conditions of Experiment 2: proportion of preferred-hand use for the nine (sequentially presented) object positions.

Sequence (N = 15)	Left Hemisphere					Right Hemisphere			
	10°	30°	50°	70°	90°	-70°	-50°	-30°	-10°
Clockwise	0.13	0.07	0.13	0.20	0.73	1.00	1.00	1.00	1.00
Counter-Clockwise	0.07	0.07	0.47	0.67	1.00	1.00	1.00	1.00	1.00

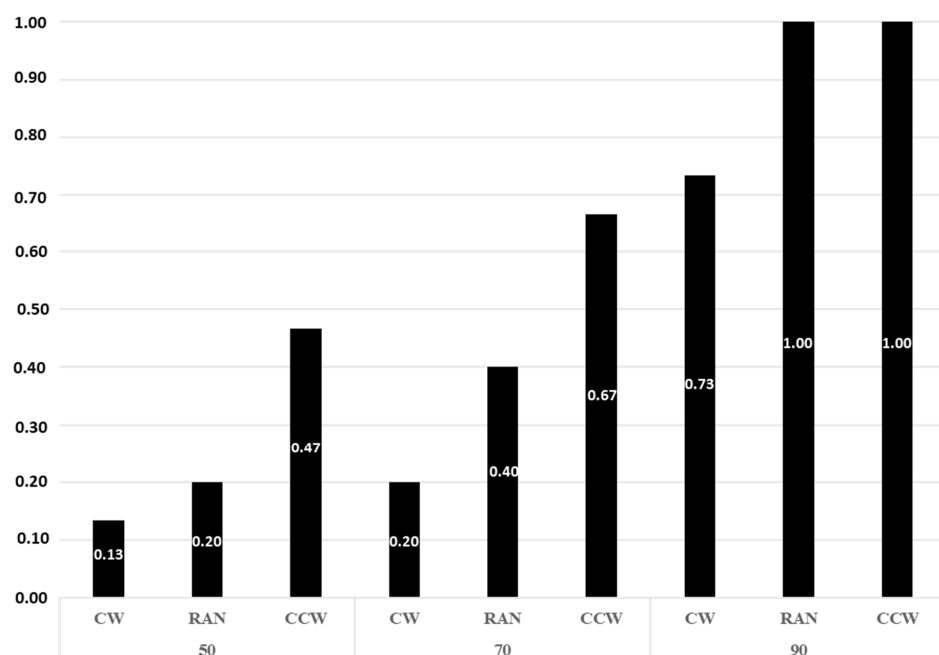


Figure 2. Results of Experiment 2: presented are the proportions of preferred-hand use for the 50° , 70° , and 90° locations for the clockwise (CW) sequence, the counter-clockwise (CCW) sequence, and the random (RAN) sequence.

As shown in Figure 2, a spatial shift in the location of the switch from preferred-hand use to nonpreferred-hand use is present between the two sequential conditions, and between the sequential conditions and the random condition. The occurrence of this effect at the level of individual participants was as follows: 67% (10 participants) displayed a hysteresis effect, whereas 33% (5 participants) had a critical boundary in their selection of limb. This result reveals the presence of hysteresis in adults’ selection of limb for unimanual grasping, identifying it as a nonlinear dynamical system.

For the participants who showed hysteresis, the average size of the spatial shift was 1.3 locations, with a standard deviation of 0.48 locations. In the critical-boundary group, one participant used her preferred hand consistently at all nine cube location in all three conditions. Another participant in this group used her preferred hand up to the 50° location in all three

conditions. The other three participants demonstrated an equal pattern of limb selection; all three switched to the nonpreferred hand at the 70° location in all three conditions.

4. Dynamic Limb Selection Model

To reproduce the effects of perseveration and hysteresis in limb selection found in the experiments, as well as the results reported in [15], a dynamic model was developed. The objective of the model was to demonstrate how discrete behavioral choices, specifically, which hand to use for grasping an object, emerge from a dynamic interplay of various, possibly time varying, external and internal factors. To accomplish this, the model will be based on a thorough analysis of the tasks, as well as on the relevant features of action selection. I will describe the model's basic features below. This will be followed by a simulation of Experiment 1 and Experiment 2. Finally, an extension of the model is presented, in which, in a straightforward, way the well-established difference in handedness strength between left-handers and right-handers is implemented. With this, the model is also able to replicate the earlier findings [15]; in particular it can reproduce the differences in the patterns of hand use between the two handedness groups.

4.1. Model Description

The core of the model consists of two 'limb-selection sites', each representing the selection process for using one of the two available hands with which to execute a reach. The sites will be assigned time-varying activation functions, $u_L(t)$ and $u_R(t)$, for the left hand and right hand, respectively. The numerical value of each site's activation function at a particular instant in time, or rather the relative proportion of both activation levels, is related to the likelihood of the choice to use the corresponding hand. The limb-selection process obeys a continuous dynamic described by a set of two coupled, first-order nonlinear differential equations:

$$\begin{aligned}\tau \cdot \dot{u}_L(t) &= -u_L(t) + h - c_L \cdot \sigma(u_R) + I_L(t) + n \cdot \xi(t); \\ \tau \cdot \dot{u}_R(t) &= -u_R(t) + h - c_R \cdot \sigma(u_L) + I_R(t) + n \cdot \xi(t).\end{aligned}\quad (1)$$

The basic structure of the model presented here is based on the general category of dynamic field models. This type of model has been used to describe various kinds of cognitive, goal-directed, and automatic human behavior, such as saccadic eye movements and arm movements [34–36], perseverative reaching movements [37–39], and spatial cognition [40–42]. The success of this type of model lies in its generality; it can be used for any number of perceptual-motor tasks without altering its basic assumptions. Note that the current model also bears some resemblance with the earlier type of model introduced by Grossberg [43]. Although the present model is itself not a *field-theoretical* model, it nevertheless incorporates two of its main features, having to do with the mapping between the continuous spatial and temporal aspects of the cube presentation, and the sudden and discrete choice to use one of the hands for grasping that cube (cf. [34]). These features are, firstly, that the choice to use one of the hands evolves gradually over time and is governed by continuous dynamics, and secondly, that these governing dynamics receive multiple inputs, which are integrated in the limb-selection process. To explain how the model integrates these features, each of the terms in the Equation (1) will be discussed in the following.

First of all, the left-hand sides of Equation (1) represents the derivative with respect to time of the activation functions u_L and u_R (i.e., du_L/dt and du_R/dt), respectively. A fundamental part of the model's behavior is its decaying property, with time constant τ . This property is implemented in the equations by adding the $-u_L$ and $-u_R$ terms on the right-hand side. In the absence of input, noise, and coupling, the activation functions will decay, eventually returning to a resting level h . This resting level establishes a basic activation level, which corresponds to an a priori willingness or likelihood to use the corresponding hand in a stimulus-free or stimulus-neutral environment. For the current version of the model, the resting level h will have an equal value for both sites.

The limb-selection sites are mutually connected by nonlinear cross-lateral inhibitory couplings. Based on earlier studies [43,44], the functional form of the cross-lateral inhibitory couplings between the limb-selection sites is that of a sigmoid shape:

$$\sigma(u) = \frac{1}{1 + e^{-\beta(u(t)-u_0)}}, \quad (2)$$

in which the slope parameter β expresses the steepness of the function, and u_0 is the inhibition threshold. The function $u(t)$ is the activation function of one of the two sites, which drives the inhibition of the other site.

This means that when the activation level of one of the sites increases (i.e., the likelihood of using the corresponding hand grows), this exerts a decreasing influence on the activation level of the other site (i.e., the likelihood of the other hand being used shrinks). The key feature introduced in the present model in order to account for laterality or lateral bias in the limb-selection process is that the cross-lateral inhibitions between the sites are inherently asymmetric. This is effectuated in the model by applying unequal coupling strengths to the two activation functions. In Equation (1), the strengths of the cross-lateral inhibitions for the sites are symbolized by the parameters c_L and c_R , for the left-hand site and right-hand site, respectively. Essential to the model's ontology is that the difference in coupling strengths (i.e., the difference in the numerical values of the c parameters) corresponds to a difference in hand preference. In other words, the more consistent the hand preference, that is, the more one hand is favored above the other, the more asymmetric the cross-lateral inhibitory couplings are. This feature will be exploited further on, in order to model differences between left-handers and right-handers. Note that in the dynamics of the model, the asymmetry in cross-lateral inhibition will only lead to an increased likelihood for using one hand over the other, not to a static preference to use one hand irrespective of external or internal stimulation.

Evidence for cross-lateral inhibition in limb selection from the handedness and laterality literature is indirect, but several studies have indicated that interhemispheric interaction and transcallosal inhibition is involved in different manual tasks [45,46]. Interhemispheric inhibition has been suggested to play an important role in unimanual actions [47]. In addition to this, other dynamic models for bistable and multistable systems have applied (asymmetric) nonlinear couplings by the same rationale, for instance, in the relative phase dynamics in bimanual coordination [48,49], dynamic field models for gaze and reaching behavior [34,37], and for transitions between unimanual and bimanual grasping [30,50].

The total input in Equation (1) consists of two distinct parts: First, perceptual input, $I^{per}(t)$, about the spatial layout of objects, unique for each limb site. In the current study, this especially concerns the object position in front of the participant on each trial. Second, memory input, $I^{mem}(t)$, representing the accumulated motor memory of previous limb selections, also unique for each limb site. This memory input builds up over the trials in an experiment. Combining the perceptual input and memory input, the total input that is fed into Equation (1) has the following form:

$$\begin{aligned} I_L(t) &= I_L^{per}(t) + I_L^{mem}(t); \\ I_R(t) &= I_R^{per}(t) + I_R^{mem}(t), \end{aligned} \quad (3)$$

for the left-hand site and the right-hand site, respectively. The nature of the two input components is based on previous research, as will be discussed below.

In general, limb selection will depend on the spatial layout of external stimulation. That is, the hand to use in a certain situation is influenced by the locations of relevant objects with respect to the actor's body. The relation between external stimulation and corresponding manual behavior obeys some very robust laws. For example, the effect of spatial compatibility in stimulus-response activity for hand use, which is related to the more general Simon effect [51] and Poffenberger effect [52]. Researchers have suggested that such spatial dependencies of reaching and limb selection might have kinetic and biomechanical

reasons, such as the costs and efficiency for reaching into hemisphere [53]. This would favor ipsilateral limb selections and entail a relatively strong ipsilateral (sensorimotor) link between hand choice and object location. In order to enable the model to exhibit such law-like behavior, the limb-selection sites will receive (perceptual) input in accordance with the lateral arrangement of the external stimulation. So, in general, the inputs for both sites will not be equal in strength, but will represent the cube's location with respect to a body frame of reference. As a result of this, changes in the likelihood to use a particular hand will arise. The strengths of the perceptual inputs to the two sites, as a function of the cube's location with respect to the participant, are presented in Figure 1 for both the left-hand site and right-hand site. In the model, the perceptual (*per*) input will be symbolized by $I_L^{per}(t)$ and $I_R^{per}(t)$, for the left hand and right hand, respectively.

Critical to the phenomena of perseveration and hysteresis, is that making choices for actions to take is a process that works on multiple timescales. To understand the results of both Experiment 1 and Experiment 2, we have to realize that the choices to use one of the hands in a particular trial, among other things, depends on the hand choices in earlier trials. Therefore, in addition to the perceptual input, a second type of input flows into the action-selection process. This input is internal to the action system (i.e., organismic [13]), and originates from the (motor) memory of limb selections in earlier trials. Starting from zero at the beginning of each condition in the experiment, this input source builds up or breaks down for each hand, depending on the particular pattern of limb selections over successive trials. Every time a particular hand is used, the strength of the memory input for that site is increased by 1.2 before the next trial. When a hand is not used in a trial, the strength of the memory input will decrease to the zero level. In the model, this memory (*mem*) input will be symbolized by $I_L^{mem}(t)$ and $I_R^{mem}(t)$, for the left hand and right hand, respectively.

The final part of the dynamics is a noise term $\zeta(t)$, which is equal for each site, and assumed to be Gaussian white noise. Noise is common in (realistic models of) behavioral, neural, and biological systems [37,54–56], representing random fluctuations in the system. The noise term basically serves as an estimate of the resultant influence of the numerous small and independent sources of neuromotor noise that might affect the limb-selection process. Noise can be of functional significance for the behavior though. In particular, under certain conditions (e.g., values of resting level, inhibition threshold) random fluctuations can lead to spontaneous reaches with any of the two hands.

4.2. Simulation Details

All simulations were performed in Matlab (version 6.1, The MathWorks Inc., Natick, MA, USA) on a standard PC. The model equations were integrated using the Euler procedure with 200 time steps of 5 ms size. This means that the simulation of a single trial spanned a time period that was comparable to the duration of making a single limb-selection in the experiments (i.e., from perceiving the cube to instantiating the reaching movement). Moreover, this was long enough to assure that the model converged to a highest activation level for a single site, which reflects the experimental procedure where participants were given ample time to decide which hand to use. Although the integration procedure equals exactly one second of the limb-selection process, at this point the model makes no specific detailed claims about the exact timing of this process.

The model statistics presented below are based on 500 runs of the model for each of the conditions in each of the experiments. In each of these runs, a complete experimental procedure was simulated for a fictive participant. These repetitions are necessary to produce a distribution of outcomes of the model, in light of the noise term of the model. The strengths of the perceptual input and memory input were set before the start of every trial. After every trial, the strength of the memory input was updated. Both inputs were present during the entire within-trial simulation, that is, all 200 time steps for each trial.

4.3. Parameter Settings and Initial Conditions

First, the model was used to simulate Experiment 1 and Experiment 2. In order to obtain a close fit with the results of both experiments, the following numerical values for the model parameters were used: the strengths of the cross-lateral inhibition terms were set to the values $c_P = 1.8$, for the preferred hand, and $c_{NP} = 5.1$, for the nonpreferred hand. Note that for lefthanders $P = L$ (left hand) and $NP = R$ (right hand), whereas for righthanders $P = R$ and $NP = L$. The steepness β of the sigmoid curve in the cross-lateral inhibition was set to 0.05, and the inhibition threshold u_0 to 0. The resting level h received a value of -0.8 . The strength n of the noise was set to 0.8. The time constant τ was set to a value of 3 s. Finally, the initial conditions were the same for each individual run of the model: $u_P(0) = u_{NP}(0) = -1.2$. Together with the (constant) resting level $h = -0.8$, this leads to a starting activation level of -2.0 .

These parameter settings were attained mostly by an active exploration of certain areas of the parameter space. The strategy followed in this mixed intuition, literature values, a thorough task analysis, and simple trial-and-error with fine-tuning. No formal parameter estimation procedure was used. Obviously, the current parameter settings are just one possible set of values that produce the desired results. Uniqueness of the parameter settings is not guaranteed, and also not to be expected (and would perhaps not even be desirable).

These parameter settings were fixed for the simulations of both experiments. Consequently, the only difference between the simulations is the order, locations, and number of cube presentations, and the corresponding perceptual input and accumulation of memory input this entails. Fundamentally, therefore, the model's account for the empirical effects of perseveration and hysteresis is based on the specific sequence of inputs to the sites, in combination with the sites' internal dynamics. After this, the original experiment [15] was also simulated to reproduce the corresponding results.

4.4. Simulation of Experiment 1

The strengths of the perceptual input were set to the values corresponding to the (-10°) , (-30°) , and 90° cube locations, as displayed in Figure 1. So, over the subsequent trials $T_1 \rightarrow T_2 \rightarrow T_3 \rightarrow T_4 \rightarrow N_1 \rightarrow N_2$ in each of the two training conditions of Experiment 1, the perceptual input for each of the two sites was set to the following numerical values: $4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0$ for the site corresponding to the hand ipsilateral to the object, and $1.0 \rightarrow 1.0 \rightarrow 1.0 \rightarrow 1.0 \rightarrow 4.0 \rightarrow 4.0$ for the site corresponding to the hand contralateral to the object.

Table 4 presents the results of the simulations for 500 runs of each of the two training conditions of Experiment 1. Shown are the training trials and the two neutral trials.

Figure 3 presents some typical results of single-participant simulation of the training conditions of Experiment 1, in the absence of noise. Figure 3a shows a participant who received a set of four training trials on the nonpreferred hand. As shown in the plots of the N_1 trial and the N_2 trial, this fictive participant kept on using the nonpreferred hand after having been trained on this hand in trials T_1 to T_4 . Figure 3b presents a participant, also trained on the nonpreferred hand, but demonstrating no perseveration. In the N_1 trial and the N_2 trial, this fictive participant switches to using the preferred hand, despite having used the nonpreferred hand four times in trials T_1 to T_4 . In terms of the model's dynamics, this behavior results from the dynamical interplay between the perceptual input (on-line bias), memory input (short-term bias), and the preference (long-terms bias). In the two neutral trials, when perceptual input has equal strength for both sites again, the difference in memory strength that has built up during the training trials was not strong enough to overrule the hand preference.

Table 4. Results of 500 runs of the model simulating the training conditions of Experiment 1: proportion of preferred-hand use in the four training trials (T_1 – T_4) and the two neutral trials (N_1 and N_2).

Condition	T_1 – T_4	N_1	N_2
Preferred-hand training	1	1	1
Nonpreferred-hand training	0.01–0.03	0.5	0.64

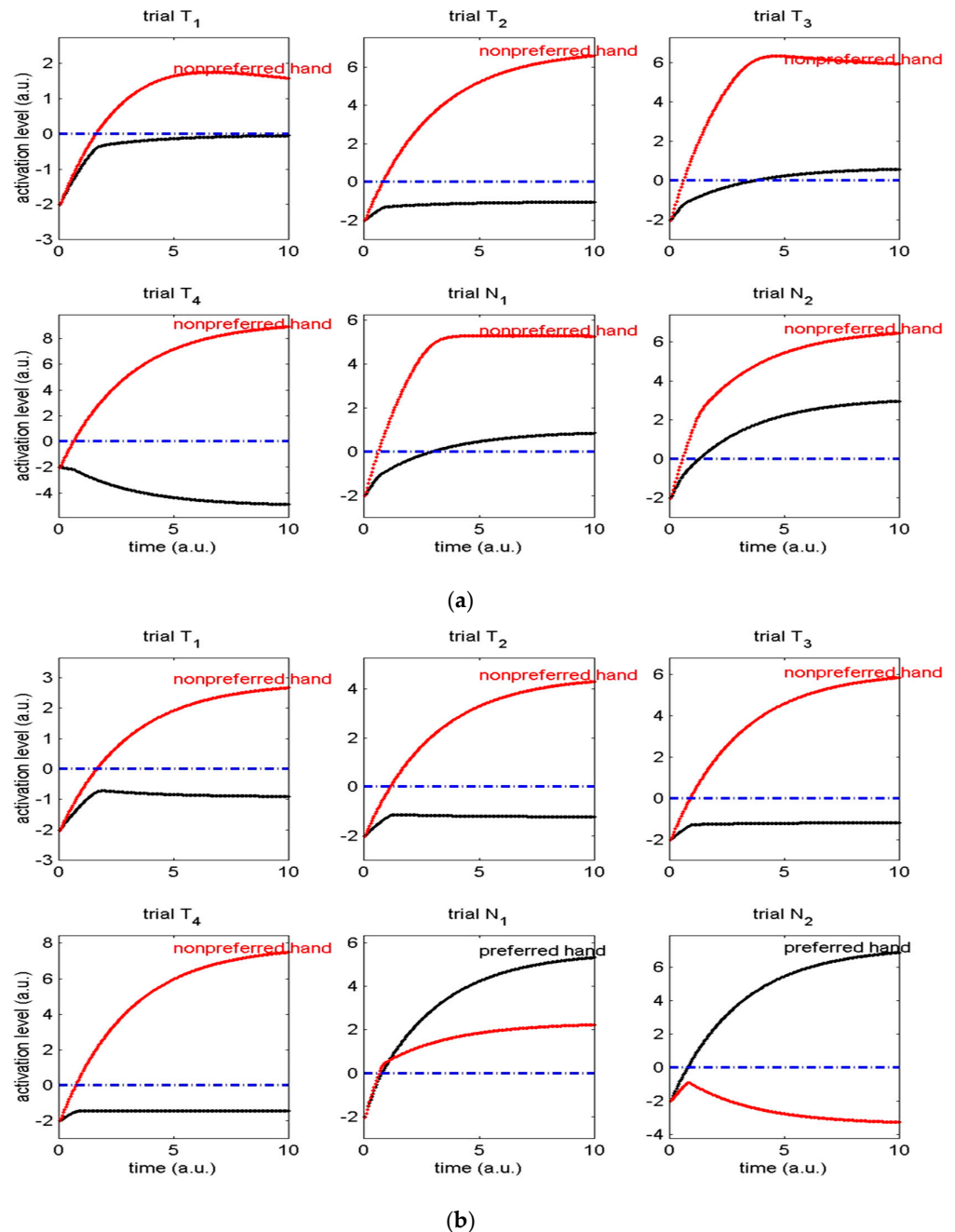


Figure 3. Examples of a single-participant simulation of the training conditions of Experiment 1. (a) Simulation of a subject in the nonpreferred-hand training task showing perseveration. (b) In the nonpreferred-hand training task showing no perseveration. Each panel represents the time evolution of the model during a single trial, over the subsequent trials $T_1 \rightarrow T_2 \rightarrow T_3 \rightarrow T_4 \rightarrow N_1 \rightarrow N_2$. Indicated at the end of each panel is the selected hand for the reach ('nonpreferred hand' (red) and 'preferred hand' (black)). The dotted line at the zero-level activation denotes the point at which the inhibition starts to affect the dynamics of the action-selection process. Noise was absent in these example simulations (i.e., $n = 0$), for presentation purposes. (a.u. = arbitrary units).

4.5. Simulation of Experiment 2

Over the subsequent trials $T_1 \rightarrow T_2 \rightarrow \dots \rightarrow T_8 \rightarrow T_9$ in each of the two sequential conditions of Experiment 2, the perceptual input for each of the two sites was set to the following strength: 1.0 \rightarrow 1.0 \rightarrow 1.8 \rightarrow 2.6 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 for the site corresponding to the hand ipsilateral to the location of the cube, and 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 4.0 \rightarrow 2.6 \rightarrow 1.8 \rightarrow 1.0 \rightarrow 1.0 for the site corresponding to the hand contralateral to the location of the cube. These numerical values correspond to the input strengths for each cube location, as displayed in Figure 1.

Table 5 presents the results of the simulations for 500 runs of each of the two sequential conditions of Experiment 2. Figure 4 presents some typical results of a single-participant simulation of the sequential conditions, in the absence of noise (see figure caption for more details).

Table 5. Results of 500 runs of the model simulating the sequential conditions of Experiment 2: proportion of preferred-hand use for the nine (sequentially presented) object positions.

Sequence	Left Hemisphere					Right Hemisphere			
	10°	30°	50°	70°	90°	-70°	-50°	-30°	-10°
Clockwise	0.10	0.05	0.10	0.24	0.62	0.93	1.00	1.00	1.00
Counter-Clockwise	0.08	0.08	0.32	0.62	0.96	1.00	1.00	1.00	1.00

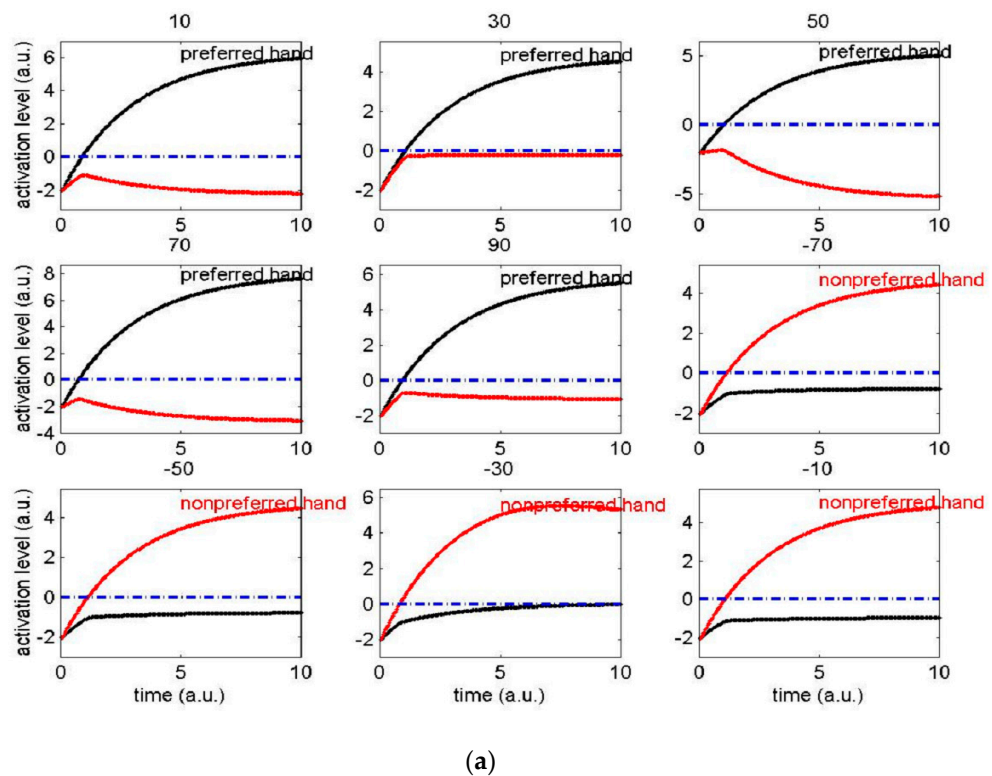


Figure 4. Cont.

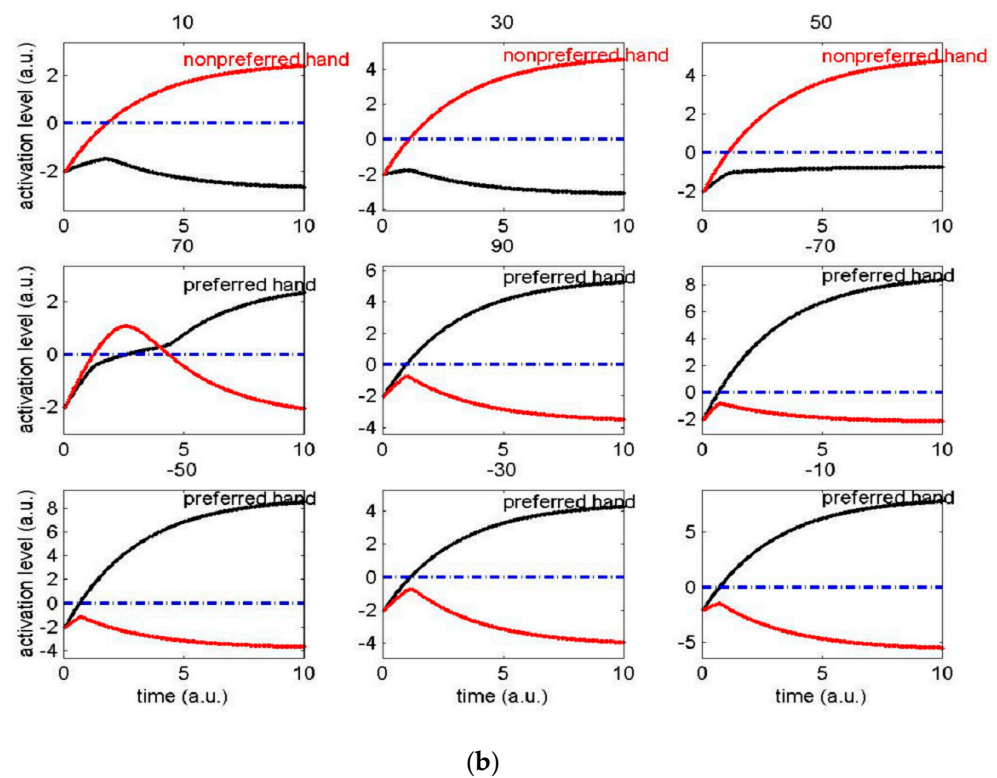


Figure 4. Examples of a single-participant simulation of the sequential conditions of Experiment 2. (a) Simulation of a subject in the clockwise task showing hysteresis. (b) Simulation of a subject in the counter-clockwise task showing hysteresis. Each panel represents the time evolution of the model during a single trial, over the subsequent trials $T_1 \rightarrow T_2 \rightarrow \dots \rightarrow T_8 \rightarrow T_9$. Indicated at the end of each panel is the selected hand for the reach ('nonpreferred hand' (red) and 'preferred hand' (black)). The exact object positions (corresponding to Figure 1) are given above each panel. The dotted line at the zero-level activation denotes the point at which the inhibition starts to affect the dynamics of the action-selection process. Noise was absent in these example simulations (i.e., $n = 0$), for presentation purposes. (a.u. = arbitrary units).

4.6. Simulation of Gabbard et al., (1997) [15]

One of the main findings of the original experiment [15] was the larger number of (across-midline) grasps into contralateral hemisphere (i.e., with respect to the dominant limb) by right-handers compared to left-handers. The researchers interpreted this finding as a difference in laterality strength between the two handedness groups. A straightforward implementation of this difference in laterality strength in the context of the model presented here, is in terms of an inequality in the asymmetry between the cross-lateral inhibition strengths for the two handedness groups. Such differences in asymmetries have been pointed out by other researchers [48,57–61]. A larger numerical difference between the two c parameters represents stronger laterality, and would therefore correspond to right-handers. Similarly, a smaller numerical difference, representing weaker lateralization, would correspond to left-handers. More generally, I propose a positive (most likely nonlinear) relation between the extent of the cross-lateral inhibition asymmetry and the degree of handedness (cf. [62]).

For the present simulations, the numerical values of the parameters were set as follows: $c_L = 1.8$ and $c_R = 3.8$, for left-handed participants, and $c_L = 5.1$ and $c_R = 1.8$, for right-handed participants. Except for the cross-lateral inhibition strengths, which I will now treat as characteristic for each handedness group, all other parameters had the same numerical values as in the previous simulations. Simulations were performed for both handedness groups separately. Following the original experimental procedure, the nine locations were simulated in random order on each run.

The bottom part of Table 1 shows the average results over 500 runs of the model simulating the original experiment [15]. As can be seen by comparing the simulation results to the experimental results displayed in the upper part of Table 1, the overall pattern of hand use is similar between the two.

5. General Discussion

This paper serves two main goals: first, I wanted to add to the empirical realm and theoretical discussion on limb selection, the aspect of multiple-timescale dynamics, exemplified by the effects of perseveration and hysteresis. In two experiments I manipulated the series of prior hand choices that preceded the selection at some point of a limb for grasping a small object positioned in hemispace. The results of the experiments showed that both perseveration and hysteresis are fundamental in adults' unimanual grasping behavior. Both phenomena are considered as basic for nonlinear multitimescale dynamical systems. As a result, these experiments revealed that limb selection is governed by an action-selection process that is both dynamical and working on multiple timescales.

Second, I set out to introduce a working dynamical model for limb selection. By integrating and extending earlier proposed mechanisms [21,22], I constructed a dynamical model that brings together various aspects relevant for action selection in goal-directed behavior. The model is capable of letting a single choice, leading to an overt behavioral selection, emerge from various underlying influences. External (i.e., task and environment) constraints, as well as internal (i.e., organismic) constraints are combined in one concise framework, working on at least three different timescales: on-line (perceptual input and the main process itself), short-term (prior choices/system's recent history), and long-term (preferences/functional or structural system characteristics). With the model simulations that replicated ours and other experimental results, I demonstrated that a dynamical view of limb selection is not only plausible, but offers a concise and rich framework for further studies in this and adjacent fields.

Below I will discuss some of the model's key aspects and the role they play in the dynamics. Before this, however, an important observation regarding the model, which indeed serves as an important criterion for all models, is that there is no one-to-one mapping between parameter settings and effects. Parameter settings alone cannot completely explain the richness of results the simulations were able to reproduce. For example, an important set of free parameters is the input strengths to the sites. These of course very much drive the sites' activation levels, and, therefore, to a large extent, determine the frequency distributions found in the simulations of the original experiment [15]. Differences in these input strengths between the sites, however, cannot explain the success of the model in replicating the effects of perseveration and hysteresis. Importantly, perseveration and hysteresis were not added to the mathematical implementation of the model as separate elements, as is done in some other models [63]. Fundamental to both the experimental effects and the modeling results, is the sequential order of the trials in combination with the multitimescale dynamics of the action-selection process.

The difference in the cross-lateral inhibition strengths of the two sites is primarily responsible for the qualitative difference between the two laterality groups at the behavioral level. Handedness, therefore, is treated as a structural property of the dynamics governing limb selection. Motor memory, in contrast, is treated as an input source that itself builds over an intermediate timescale with respect to the dynamics of the planning process. The dynamic reshaping of the action-selection field by the motor history of the system (memory trace) has already been introduced in the dynamic field theory [34,37–39,64]. A novel aspect of the present model is that it incorporates a structural or functional asymmetry of the action system (long-term bias) as an integral part of its dynamics, alongside other constraints operating on different timescales.

5.1. Action Selection, Perseveration, and Multiple Timescales

Building on earlier work [5,34,37,65–68], a view on action planning and action control has been proposed that conceives of them both as a combined, ongoing, and dynamical action-selection process for actions to take [69–72]. Although already elaborated on earlier, the basic features of this conceptual model of action selection will briefly be described in more detail below. The model's main features are: First, choices for action are multicausal, which means that many factors on several timescales can (potentially) influence the choice that will be made. These factors can be of very different origin and nature. Second, the process is embodied and embedded (situated) in its nature. This means that action selection, at its most fundamental level, is organized by and deals with structural and functional characteristics of the actor's body and environment. These include preferences of a functional, biomechanical, or neuro-anatomical nature. Third, the process has intrinsic dynamics that incorporate these properties and determine the fate of the relevant factors in the process, in accordance with the neuro-anatomical structure of the action system. This makes it a continuous dynamical system in which choices for action emerge gradually over time. A fourth distinctive property, although not the topic of this paper, is that the process is also continuous, in the sense that it does not halt after a single choice is made. Rather, the dynamics of the process continues to generate subsequent choices for action, fed by the available input that may have changed. Choices are not ready made, waiting to be executed, but emerge from and remain part of the dynamics of the process. In this paper, I have built on the view of planning described above to model limb selection.

One of the most elaborate models embracing a highly similar view is the model for perseverative reaching behavior in infants, better known as the A-not-B error [37,73]. The A-not-B error entails an infant's perseverance in reaching towards location A, after a number of successful reaches to that location, even after a clear perceptual cue is given in favor of another location (i.e., location B). Essentially, the A-not-B error and the phenomenon of perseveration in general demonstrates that a choice for action at a certain point in time is affected by previous choices for actions, such that these temporarily overrule the perceptual information that is available. It is a most striking example, from which it becomes apparent that processes operating at different timescales (as mentioned above) interact. Perseveration as a more general cognitive or behavioral phenomena, revealing the multiple-timescale dynamics of planning, has not had a lot of attention from researchers in the behavioral sciences. There are some studies on children's search behavior [74], sorting [75], word-naming [76], categorization [77], and task-switching [78]. To our knowledge, the present study is the first which explicitly addresses perseverative limb selection in adults (however, see [79–82]).

The model for the A-not-B error is based on dynamic field theory of movement preparation [34]. A key aspect of the model is that the planning of a reaching movement is a process that takes place on different timescales. In the A-not-B task there is the within-trial timescale of the evolution of a motor plan for a single reaching movement towards a certain location. This plan is influenced by various types of information (task and specific inputs) that are available in real time, that is, before reaching onset and during the actual planning of the reaching movement. In addition to this, an over-trials timescale of a series of reaching movements is suggested. At this timescale, a motor memory evolves, which builds up a short-term bias towards a particular location, each time a reach is executed in the direction of that location. In other words, shaped by these earlier reaching movements, the motor memory gradually builds over time. In the authors' perspective. this motor memory influences subsequent plans for reaching movements.

A novel aspect introduced in the present paper is the aspect of an asymmetry or a preference in the action-selection process. From the perspective of multiple-timescale dynamics, it is interesting to analyze the way in which a long-term bias potentially influences the planning. Within the focus of this study, hand preference is such a long-term bias, known to affect limb selection. This asymmetry arises over a developmental timescale determined by factors that are not yet fully understood [9–11,83]. Nevertheless, its influence cannot

be denied, and must be taken into account in any serious model for limb selection. A fundamental reason why this could be of more general interest for cognitive science is that it gives us a glimpse at how preferences as functional or structural asymmetries are part of the perception-action cycle, at the level of planning in goal-directed behavior.

5.2. A Primer on Modeling Developmental Change

As is well-known, handedness consistency in children continues to grow until at least three years of age, and probably beyond [9–11]. Moreover, from other fundamental work, we know that the direction of handedness undergoes a series of transitions in the first few months after birth [84,85]. Related to the issue of structural or functional asymmetry discussed above, the concept of cross-lateral inhibition in the action-selection process gives rise to an interesting new perspective on the development of handedness and hand preference. Within the proposed model, age-related changes in hand preference can be implemented by an increasing asymmetry in cross-lateral inhibition, that is, by an increasing numerical difference between the strengths of the inhibitory connections [71,86]. This hypothesis might be a way to link handedness to more general developmental changes associated with lateralization. However, much is still to be discovered, and predictions are that research on the development of handedness is likely to see some major changes in the years to come [83].

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Conflicts of Interest: The author declares no conflict of interest.

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