

Joint Action Enhances Motor Learning

by

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ABSTRACT

Learning a novel motor pattern through imitation of the skilled performance of an expert has been shown to result in better learning outcomes relative to observational or physical practice. The aim of the present project was to examine if the advantages of imitational practice could be further augmented through a supplementary technique derived from my previous research. This research has provided converging behavioral evidence that dyads engaged in joint action in a familiar task requiring spatial and temporal synchrony end up developing an extended overlap in their body representations, termed a joint body schema (JBS). The present research examined if inducing a JBS between a trainer and a novice trainee, prior to having the dyad engage in imitation practice on a novel motor pattern would enhance both of the training process and its outcomes. Participants either worked with their trainer on a familiar joint task to develop the JBS (Joint condition) or performed a solo equivalent of the task while being watched by their trainer (Solo condition). Participants In both groups then engaged in blocks of alternating imitation practice and free production of a novel manual motor pattern, while their motor output was recorded. Analyses indicated that the Joint participants outperformed the Solo participants in the ability to synchronize the spatial and temporal components of their imitation movements with the trainer's pattern-modeling movements. The same group showed superior performance when attempting to freely produce the pattern. These results carry

significant theoretical and translational potentials for the fields of motor learning and rehabilitation.

TABLE OF CONTENTS

	Page
LIST OF FIGURES.....	vi
CHAPTER	
1 INTRODUCTION	1
2 METHODS	34
3 RESULTS	42
4 DISCUSSION	62
REFERENCES.....	70

LIST OF FIGURES

Figure		Page
1.	Apparatus for the Joint Task	21
2.	Left Hand Inverse Efficiency in Study 1	25
3.	Right Hand Inverse Efficiency in Study 1	26
4.	Left Hand Inverse Efficiency in Study 2	27
5.	Right Hand Inverse Efficiency in Study 2.....	28
6.	Time Series of Ideal Pattern.....	36
7.	Time Series of Pattern Imitation (1)	37
8.	Time Series of Pattern Imitation (2)	38
9.	Training Spatial Cross Correlation of Trainer and pattern	47
10.	Training Spatial Cross Correlation of Participant and Trainer	49
11.	Training Temporal Cross Correlation of Participant and Trainer	50
12.	Training Efficiency Cross Correlation of Participant and Trainer	52
13.	Learning Spatial Cross Correlation of Participant and Trainer ..	54
14.	Learning Spatial Cross Correlation of Participant and Pattern .	56
15.	Training Hand deviation along X axis	58
16.	Training and Learning Hand deviation along X axis	60

CHAPTER 1

INTRODUCTION

The acquisition of new motor skills through imitative practice has recently gained revived attention in the field of motor learning. It has been demonstrated that observing a human model perform a target pattern prior to practicing the execution of that pattern yields better motor acquisition, relative to solo practice (Ashford, Bennett, & Davids, 2006). The positive effects of this imitative practice has been attributed to the neuro-physiological and behavioral finding that action observation taps into the same neural substrate and exploits the same informational architecture deployed during action execution (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). Resonance of the cortical and cortico-spinal motor components during observation facilitates subsequent execution, and this dual initiation of the motor system mediates the learning advantages of the imitative-practice training paradigm.

The primary aim of the proposed project is to introduce, and examine the relative effectiveness of, a supplementary motor-training technique that could potentially augment the advantageous learning outcomes already documented for imitative practice. This supplementary technique stems from ongoing research in our laboratory (Glenberg & Soliman, 2013; Soliman, Ferguson, Dexheimer, & Glenberg, under review), in which we show that co-actors engaged in a joint task requiring fine spatiotemporal coordination end up developing a joint-body schema (JBS). The JBS is characterized by a strong interpersonal overlap in the

multisensory and sensorimotor representation of the body parts of the actor and his or her partner. This representational overlap outlives the initial joint task and induces interpersonal sensorimotor coupling for a period past its completion. In the current project, the aim is to empirically examine if this extended JBS interpersonal state could be exploited to improve the outcomes of motor practice and learning through imitation. Specifically, the project will test if JBS-supplemented imitative practice, relative to standard JBS-free imitative practice, results in better motor-learning outcomes

In the first section below, I outline the major theories of motor learning. In the following section, I review research pertaining to the relative effectiveness of the different motor-practice modes: solo physical practice, observational practice and imitative motor practice. I then explicate the characterization of the JBS construct as revealed by previous research, and highlight its potential for enhancing motor learning. Finally, I conclude the chapter by a formulation of the specific research questions addressed by the study comprising the project.

1.1 What is Motor Learning?

Acquiring a new motor skill is a complex process that requires the motor system to solve a number of problems. Learning to serve or return a serve of a tennis ball, for example, requires optimizing the amplitude, direction, and temporal schedule of the force command sent to the appropriate effector, all while taking into account random and systematic variability that the neural signal, the body, and the world introduce to every instance of executing the target motor pattern.

Coordinating among the multiple joints that are both directly (e.g., shoulder, elbow, and wrist of one upper limb) and indirectly (e.g., joints of the other upper limb and lower limbs) involved in serving the ball is another problem set that the system needs to solve to accomplish skilled performance. Selecting appropriate elementary motor primitives and assimilating these into a fluent action pattern or sequence of patterns is another task that skilled performance of a guitar or piano chord, for example, necessitates.

In explaining how the system solves these problems, theories of motor learning could be roughly divided into cognitive and dynamical theories. The former emphasizes mechanisms of learning that, at least in principle, could be implemented in the various sensory and motor areas of the brain, while the latter place the locus of interest in the dynamical interactions among the spinal motor neurons and muscle synergies. Given that the proposed project pursues questions pertaining to the enhancement of motor learning due to manipulation of internal bodily representations, the review here will be limited to the former class of motor-learning theories.

One of the early cognitive theories is Schmidt's (1991, 2003) schema theory. This argues that the acquisition of a motor skill involves, first, the incremental development of a "generalized motor program" (GMP) that codes the invariant properties of relative timing and relative force that are uniquely defining for the target motor pattern. The GMP for drawing the letter "S", for example, specifies the amount of force over time that the elbow, wrist, and hand joints follow to

produce the target pattern, irrespective to whether the “S” is a small one on a sheet of paper or a large one that fills up a blackboard. In a second stage, learners acquire a parameterization schema that allows scaling of motor programs to the task specifics and environmental demands. Learning along both of these two lines involves mapping of the parameters chosen upon the execution of many instances of a given action pattern onto the sensory and spatial outcomes of these respective execution attempts. A skilled state is achieved when a “rule” that optimally describes the relation between these two variables is in place.

Another cognitive theory of motor learning assumes that skilled performance is achieved via sensorimotor adaptation of “internal models” (Wolpert & Kawato, 1998). These models predictively code the sensory consequences of motor commands (i.e., forward models) and, reversibly, predict the motor command required to achieve a given sensory goal (i.e., inverse models). Inverse models are especially instrumental in motor control of skilled behavior, as they compute parameters of the motor command required to achieve a desired, spatially defined, prospective body states. Forward models are thought of as very instrumental during learning of new skills. Novice performance is characterized by a greater error in the prediction of the sensory consequences of a given motor command. Through practice, comparison of consequent sensory feedback and antecedent sensory prediction leads to a gradual reduction of the prediction error in the relevant forward model. Thus, a skilled performer is one who generates an

optimal forward model that predicts the sensory consequence of the target motor command with minimal, or no, error.

1.2 Types of Motor Practice

1.2.1 Physical Practice

Repeated attempts to execute a target motor pattern is by far the most common practice method for acquiring a motor skill. Research on the effectiveness of physical practice focuses on variables that are partly drawn from the theoretical postulates of the above motor-learning models as well as on general learning and general memory variables. For example, whether, and in what frequency the trainee should receive information on her success in meeting the spatial goal of a motor pattern after attempting to produce it is one critical variable that reflects the above models' emphasis on the role of feedback in developing a GMP, a scaling motor schema, or a forward model (Schmidt, 1991). The effect of randomly intermixing practice trials on the target and no target motor patterns (vs. blocked practice) on the acquisition rate, retention, and transfer of the target motor skill is another variable commonly investigated in the literature (Brady, 1998). The temporal spacing of motor practice sessions is yet another variable that determines the quality of performance in retention tests (Shea, Wright, Wulf, & Whitacre, 2000). And, obviously, the amount of practice, difficulty of the task, and initial skill level (Newel & Rosenbloom, 1981) are intuitive variables that influence the acquisition of motor skill through physical practice.

1.2.2 Observational Practice

Practicing a target motor skill through mere passive observation of the pattern being modeled has long been found to produce reliable learning outcomes (Landers, 1975). Early interpretations assumed that observational practice facilitates learning through the construction of a higher-cognitive “symbolic” mental model of the task that is later “translated” into motor code to overtly guide physical practice (Bandura, 1986). This a modal interpretation of the beneficial role of observation has fallen out of favor, and gave way to a perceptual account in which learners are assumed to develop spatial schemata of the target pattern - during observation (Hikosaka et al., 1999; Howard, Mutter, & Howard, 1992; Shea et al., 2000). While originally taking up a perceptual code, the schemata are later covertly used to guide motor programming during physical practice (Hayes, Andrew, Elliott, Roberts, & Bennett, 2012).

A third, competing, account argues that sensory-motor translation is not as delayed as assumed by the above account, but that the motor system is covertly engaged during the observation of modeled action (Vogt, 2002; Heyes & Foster, 2002). Evidence that memory traces acquired during observation are encoded motorically from the outset comes from a number of behavioral and neurophysiological studies.

Bird and Heyes (2005) showed, for example, that participants who passively observed a human model train on a key-press sequence with one set of fingers showed learning gains when later tested on producing the pattern, but only when

they used the same finger set they had observed the human model use. If initial coding during observation is purely perceptual-spatial, using either the same or different set of digits should not have influence translation during the execution phase. Mattar and Gribble (2005) showed that participants who watched a model learn how to move a robotic arm against systematic perturbation (i.e., adaptation to a motoric force field) showed execution advantages later when performing the same task. Importantly, these advantages disappeared when learners engaged in a motor, but not a cognitive, interference task during observation.

Classen and colleagues (Classen, Liepert, Wise, Hallett, & Cohen, 1998) demonstrated that the primary motor cortex (M1) develops a short-term memory of recently practiced motor patterns. A transcranial magnetic stimulation (TMS) pulse applied to the thumb area of the participants M1 at baseline indicated whether the dominant response was thumb flexion or extension. Participants then repeatedly practiced a unidirectional motor execution of the thumb movement opposite to that indicated at baseline. Post-practice TMS applied to the same M1 showed a reliable tendency towards thumb movement in the trained direction. Importantly, Stefan and colleagues (Stefan et al., 2005) recently replicated the same M1-based motor trace development with participants who passively observed, rather than executed, the thumb movements during training. The immediate sensorimotor-translation account of observational practice rests on the often-replicated finding that action perception and action execution implicate a common fronto-parital neural circuit encompassing the frontal

premotor and inferior parietal areas of the brain (Caspers, Zilles, Laird, & Eickhoff, 2010; Rizzolatti & Sinigaglia, 2010). This circuit, dubbed the mirror neuron system (MNS), is believed to tap into the motor repertoire of the perceiver to simulate the observed action, and results in a subthreshold peripheral resonance that is temporally and anatomically faithful to that action (Gangitano, Mottaghy, & Pascual-Leone, 2001; Rizzolatti & Craighero, 2004).

With novel skills that have no trace in the observing-learner's motor repertoire, central simulation and peripheral resonance is believed to initially involve the elementary motor constituents comprising the action pattern (Buccino et al., 2004; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Frey & Jerry, 2006; Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012; Vogt et al., 2007). In these five studies, observational learners of complex motor patterns showed reduced MNS activity while attempting to execute the pattern after the practice sessions relative to before the practice sessions, and this activity reduction was not evident for novel, but unpracticed, homologous motor patterns. This reduction is taken as an evidence for the involvement of the MNS and the concept of motor simulation/resonance in observational learning. The reduction is thought to reflect enhanced neural efficiency that accompanies the integration of the simulated motor constituents into a motor gestalt or a holistic form through repeated, concurrent component simulation during practice.

1.2.3 Imitational Practice

In imitation practice, learners attempt to match a modeled action pattern either concurrently or shortly after they observe it unfold. This typically involves alternating short cycles of observation and execution. Imitation practice seems to result in greater learning gains relative to either physical or observational practice.

Stefan and his colleagues (Stefan, Classen, Celnik, & Cohen, 2008) used the same paradigm as in their (2005) experiment to compare the strength of the M1 memory trace developing through imitative and physical practice. Relative to pre-training TMS-evoked thumb MEPs, the study showed a greater probability for the post-practice TMS pulse at M1 to evoke thumb movement in the trained direction after imitative than after mere physical practice. Participants in a ski-simulator (Whiting, Bijlard, & den Brinker, 1987), after five days of practice, showed more fluent bimanual coordination when they had practiced while watching an expert skier modeling the target action than when they were left to discover the target pattern unguided. Cross and colleagues (2009) trained participants for five days on multi-step dance sequences by having them watch and practice executing the target step positions displayed in short video clips. For some sequences, the step positions were cued symbolically by arrows at the target locations (a physical practice condition by current review standards), while the rest of the dance sequences were demonstrated by the leg of an expert human dancer cueing the target locations comprising the sequence (imitation practice). Relative to an

unpracticed sequence, both physically and imitatively practiced sequences were more accurately and rapidly performed in a post test. Importantly, however, imitative practice led to significantly higher learning gains relative to physical practice.

A study that directly compared all three types of practice showed the superiority of imitative over both observational and physical practice (Blandin et al., 1999). A pilot study was first used to map the relative timing of a four-segment hand-transport task requiring participants to lift their hands from a base then knock down three wooden barriers and finally place the hand at a pre-determined end position. The experiment then trained participants on an artificial relative-timing schedule of the task segments that differed significantly from the natural schedule established by the pilot work. Some participants practiced by physically performing the artificially-scheduled hand-movement segments, others practiced by watching them, and a third group had a combined observational and physical practice. The performance of this latter group (i.e., resemblance to the trained artificial movement schedule) was significantly greater than in the other two groups.

This relative advantage of imitative practice could be attributed to the stronger involvement of the MNS during imitation. This is because both of the observational and executional phases of the imitation cycle presumably fall within the firing scope of the MNS system. Iacoboni and his colleagues (1999) asked participants to passively watch a finger-lifting movement (i.e., observation

condition), to lift their finger in response to a symbolic cue (i.e., execution), or to lift their finger in response to a finger-lifting cue (i.e., imitation). Event-related brain imaging showed the highest activity of the MNS during the last condition. Subsequent neurophysiological reports confirmed this finding, and extended its validity to more complex hand and arm imitative responses (Grèzes, Armony, Rowe, & Passingham, 2003; Tanaka & Inui, 2002).

Neurophysiological studies examining the role of the MNS in motor learning of multi-component patterns (e.g., guitar chords) also confirm the superiority of imitation practice. Buccino and colleagues (2004) showed that, during training, the MNS is more active when participants watch the target guitar pattern with the intention of subsequently executing it (i.e., in the imitational practice condition) than when viewing the pattern without an intention of subsequent execution (i.e., in the observational practice condition). In addition, the pre-to-post-practice reduction in MNS activity evident when participant attempt to produce the target pattern, which is reported as an effect of observational practice above, is significantly more pronounced for imitation than for observational practice (Higuchi et al., 2012). Note that these two result sets are not in contradiction; one indicates the neural signature of simulation during training and the other shows the signature after acquisition is completed.

Finally, it is important to note that the MNS-mediated simulation advantage of imitation is not likely due to the trivial feature of the presence of two instances of the target stimulus in an imitation trial (i.e., the model's moving hand and the

participant's moving hand) which is inherently absent in observational learning (only the model's hand) or in physical practice (only the participant's hand). Buccino et al.'s (2004) result, reported above, speaks against this possibility as it shows a resonance advantage right during the observation sub-phase of the imitation cycle, and this result is also confirmed during observation of familiar action with and without the intention of subsequent execution (Grezes et al., 2003). Nor is it likely that the advantage of imitation is solely reliant on the presence of two instances of the target spatial goal of movement. Heiser and colleagues (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003) asked participants to move their fingers upward in response to either a dot moving upward (i.e., spatial goal) or a finger moving upward (i.e., means and goal of movement). Repeated TMS applied to the frontal node of the MNS (i.e., Pars Opercularis) selectively disrupted imitation in the finger-cue condition. A homologous finding in the context of motor learning of complex action sequence was recently provided by Boutin and colleagues (Boutin, Fries, Panzer, Shea, & Blandin, 2010). Participants physically practiced performing the target sequence after observing either the target spatial locations sequentially illuminated or the sequential illumination plus the associated hand flexion and extension. Post-practice tests found significantly better learning of the sequence in the latter condition.

But if the above two features are not the ones endowing imitation its advantageous status, what is so special about imitation, then? Why is it

accompanied by higher motor resonance? And, why does it lead to better learning? The likely processes operative during imitation, which explain its being accompanied by higher resonance activity relative to passive observation, and its more effectiveness in promoting learning relative to both observational and physical practice probably pertain to concurrent motor and somatosensory resonance. When one observes a peculiar and novel hand movement with no intention of immediately replicating it, the motor system gets moderately active due to moderate resonance of the MNS. But when an intention of immediate replication is present during observation, the modeled action likely induces not only motor resonance, but is also used to run a continuous kinesthetic image that simulates how the modeled action will “feel like” as I will shortly try to replicate it. This kinesthetic simulation likely feeds into, and augments the motor resonance, resulting in the higher MNS activity evident in the above studies. There is evidence supportive of this kinesthetic-image surplus hypothesis in the literature (Buccino et al., 2001; Grezes, 1998; Iacoboni et al., 1999). In all of these three studies, activation of the superior parietal lobule was reported when participants observe an action with the intention of imitating it and absent when observing the action without the replication intention. This area is known to be active during somatosensory and proprioceptive imagery (Rizzolatti & Craighero, 2004). In addition, both the visual copy of the modeled action perceived in real time and the kinesthetic copy simulated internally by the learner a) reinforce each other and b) provide the components of the sensory “forward model” stipulated by

Wolpert for the acquisition of a motor skill. In fact, when the learner starts to execute the novel action immediately after perceiving it, the implicit computations of the predicted sensory outcomes of the attempted force output will be likely more accurate as they are guided by the visual image and kinesthetic image that will likely be still active in working memory. This might explain why learning of the forward model proceeds faster in the imitative, relative to the observational and physical, practicing paradigm.

It follows from the above that manipulations that augment the sensorimotor resonance of the learner's system during imitation might enhance the learning outcomes of this practice method. Recently, we have experimentally demonstrated that indeed sensorimotor resonance with the perceived postures and actions of others could be augmented through the induction of what we term a joint body schema between the perceiver and the perceived through joint action. Since the aim of the current project is to explore the effectiveness of supplementing imitative motor practice with a joint body schema, I now review this construct.

3. What is the Joint Body Schema and How it may Enhance Imitative Motor Learning?

3.1 What is the Body Schema?

The body schema is a structured model of one's own body that keeps implicit spatial representations of the dimensions and relative positions of its various segments (Graziano & Botvinick, 2001; Head & Holmes, 1911; Reed & Farah,

1996). These spatial representations are modular, for example, the right thumb and right index finger are two independent sensorimotor units. At the same time, the representations are hierarchical and relational, for example, the range of spatial configurations the two fingers can assume is biomechanically constrained by their extension from the same hand, whose position and posture are in turn constrained by the relative posture of more proximal segments of the limb and the limb's position relative to the torso (Graziano, Cooke, and Taylor, 2000; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

Spatial encoding of the body schema is multisensory, integrating primary visual, tactile, and proprioceptive afference in several cortical foci across the parietal and frontal lobes (Maravita, Spence, & Driver, 2003; Medina & Coslett, 2010). Single cell recording in monkeys (Duhamel, Colby, & Goldberg, 1998; Hyvarinen & Poranen, 1974; Rizzolatti et al., 1981 a, b) and neuroimaging in humans (Serenio & Huang, 2006) have identified several neural circuits with bimodal receptive fields centered around body parts. These neural assemblies fire upon presentation of either tactile stimulation of a given body part, or visual stimulation at or around the same part. And, the visual receptive field of these circuits dynamically tracks the corresponding tactile receptive field across changes of the posture and position of the relevant body part (Graziano & Gross, 1995; Kennett, Eimer, Spence, & Driver, 2001; Kennett, Spence, & Driver, 2002). That is, in principle, the neuron that fires when your right thumb is touched while on the

right side of your body would also fire upon visual stimulation next to the thumb after it has moved to the left side of your body.

The spatial parameters of this dynamic bimodal model of the body are continuously reset based on the two-way flux of information to and from the motor system (Wolpert & Ghahramani, 2000; Buxbaum, Giovannetti, & Libon, 2000; Desmurget et al., 1999). To grasp a cup, for example, the motor system first adapts the current values instantiated in the spatial parameters of the bimodal hand representation to incorporate its starting position and posture. It factors these into the motor plan, which specifies the required schedule of muscle forces needed for the transport and grasp components of the intended action. An efference copy then projects how the hand should feel and look like on route, tapping into the bimodal spatial parameters of the hand. As the motor program executes, the projected spatial parameter values of the hand schema are compared to the actual values channeled in real time through multisensory afference, and discrepancies are reported back to the motor system to modify the force schedule. In fact, this interplay between the muscular force parameters (i.e., on the motor system's side) and the multisensory spatial parameters (i.e., on the side of the body schema) also underlies performance of implicitly simulated or explicitly imagined action (Parsons & Fox, 1998; Schwoebel, Buxbaum, & Coslett, 2004), a feature that is crucial for the JBS development.

3.2 What is the Joint Body Schema?

The hypothesized joint body schema (JBS) is an adapted body schema whose spatial parameters acquire values representative not only of the current position and posture of one's own body part, but that of the homologous body part of a task partner as well. It is "joint" in the sense that it exploits the neural machinery attached to one body to implicitly keep track of the position and posture of two separate bodies, one's own and one's partner's. The joint body schema emerges incidentally in the context of joint action tasks, particularly of the type requiring the collaborating partners to tightly coordinate the movements of their bodies, in space and across time, to achieve and maintain optimal performance.

It is not a joint task schema, however. That is, once it emerges among dyads in the context of a given joint task, it outlives the task and continues to induce implicit spatial representation of the task partner's body for some time past the dyadic interaction. In addition, it is not constrained to the specific percepts and motor programs experienced by the dyad during the initial joint task inducing it. That is, whether the partners later view one another's stationary bodies, get engaged each independently in their own individually-framed task, or even collaborate on a new task that bears no conceptual or sensorimotor resemblance to the initial task, the JBS would still be in effect. That is, visually perceived information specifying the position and posture of a former task partner's body will continue to be mapped onto the multisensory representation of one's own

body for some time, inducing implicit, task-neutral, and temporally extended spatial entanglement with the partner's body.

Consider a two-handed task, such as carrying a basket or sawing a tree trunk, for which one partner (A) uses the right hand and the other (B) uses the left hand.

Prior to engaging in the task, A might have expectations about how to cooperate.

But as soon as the task starts, A's performance of her share in the task needs to be guided by the real time flow of information about her partner's role in the task.

One obvious source of information is perceptual: A uses visual, auditory, and proprioceptive information specifying her partner's left-hand movement to adjust her own right-hand movement towards smooth interpersonal coordination.

Importantly, however, we propose that A uses, in addition, her own body as another source of information to solve the coordination problem. That is, the visually perceived kinematics of B's left hand is modeled by the multisensory spatial circuits underlying the body schema of A's inactive left hand. The mirror-neuron system (MNS, Rizzolatti & Craighero, 2004) then kicks in. The motor controllers of A's left-hand simulate the dynamic forces underlying B's perceived hand movement, guided by the spatial parameter values instantiated in A's own left-hand body schema. This motor simulation, in turn, enforces the dyadic sensory model developing in A's left hand schema (i.e., the JBS).

Through this simulated sensorimotor loop, A acquires a bodily source of information that could partially guide the executed movement of A's own right hand towards smooth interpersonal coordination. We hypothesize that this

incipient JBS comes with incidental extended consequences: Even after the dyadic joint task terminates, the JBS developed by the multisensory spatial model of A's left hand does not instantaneously subside back into a regular body schema. Due to use-induced plasticity (as in Classen, Liepert, Wise, Hallet, & Cohen, 1998), the left hand JBS remains in effect. The perceived position and posture of B's left hand will continue to be modeled by A's left-hand neural model. If, after the initial joint task, B rests her left hand palm up on the table top, and A rests his or her own left hand palm down, the JBS of A's left hand will still instantiate parameter values of both palm up and palm down postures. If B then scratches her head with her left hand while A's left hand is stationary, A's underlying JBS will instantiate the perceived posture and position change characteristic of head scratching, now with the additional involvement of force simulation contributed by the MNS. Thus, the motor resonance of A's left hand will involve a stronger and better specified force component relative to a condition in which A had just met B. This enhanced motor resonance arises because the MNS is guided by a JBS that is already tuned to mapping the perceived spatial parameters of B's hand movement.

The hypothesized characterization of the joint body schema is empirically supported by a number of studies (Glenberg & Soliman, 2013; Soliman, Ferguson, Dexheimer, & Glenberg, under review). In four studies, we first had a participant engage with an experimenter in a joint-action task to induce the hypothesized interpersonal JBS between one of the participant's effectors and

the experimenter's homologous effector. The participant then went through a JBS examination phase to test for the emergence of the proposed JBS. The examination of the JBS was done by requiring the participant to perform a new task using the JBS-relevant effector. This second task, however, did not require the participant to coordinate performance with the former task partner (i.e., the experimenter). Nonetheless, the experimenter was present in this testing phase, and concurrently used her JBS-relevant effector to perform an incongruent version of the participant's new task. If, as hypothesized, the participant develops a JBS during the initial joint task, then the perceived position and posture of the experimenter's relevant effector will continue to be automatically mapped onto the participant's own effector during the second, individually-framed task. This mapping should then interfere with the participant's ability to perform the individual task. We also ran a between-subject control condition (Solo condition) in which participants were required to either perform (or passively perceive the experimenter perform) a solo version of the initial joint task. These participants then engaged in the same JBS measurement phase. Because no (or a greatly reduced) JBS should be formed in the Solo condition, the degree of interference should be reduced.

In all four studies, the initial joint-action task was operationalized by a five-minute joint candle-sawing activity (see Figure 1). This joint task required the participant and experimenter each to use one of their hands to bimanually and rhythmically operate a cutting wire sideways to saw candles down to their wicks. The candles

were held horizontally in a holder so that the wire rested on the upper surface, and the candles were replaced as needed for the five-minute duration.

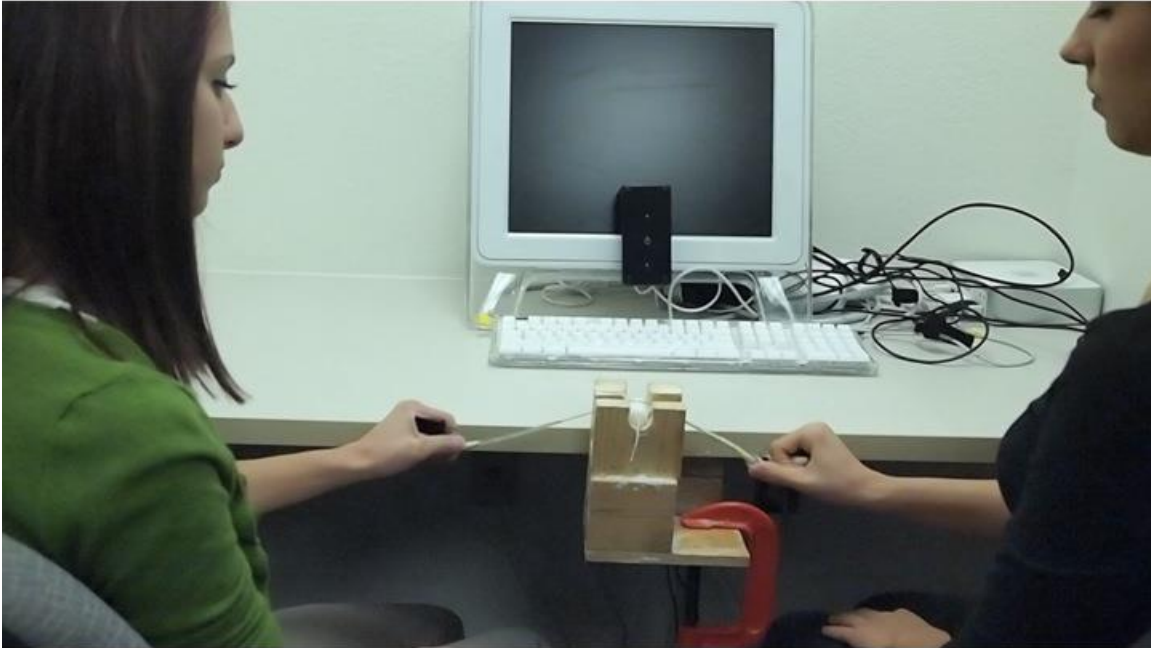


Figure 1. Apparatus used to induce a JBS in all experiments; Joint sawing condition. The candle is held horizontally in the wooden candle holder. The participant is on the right and uses her right hand to hold the sawing wire. Note that her left hand, the target for JBS induction, is in her lap. The Experimenter sits on the left and uses her left hand (the model for the induced JBS) to hold the other end of the sawing wire. The LED box is mounted on the bottom of the computer monitor.

In all experiments, a right-handed participant sat on the right side of the candleholder and an experimenter sat on the left side. When engaged in the joint-sawing condition, the participant used her right hand, and the experimenter used her left. The participant's idle left hand was always in her lap, and the experimenter's idle right hand was always in her lap. Because the wire was flexible, the task required finely tuned coordination to keep the wire taut. In the Solo control conditions, only the participant was engaged in sawing, while the experimenter sat passively and watched. In these conditions, the participant used the same hand she would have used had she been assigned to the joint-sawing condition. In this case, a plumb-line weight was attached to the end of the sawing tool to keep the wire taut.

We predicted that the seemingly idle left hand of the participant is actually engaged in modeling of the experimenter's active left hand during sawing. As such, the participant would develop a left-hand JBS encompassing his or her own left and the experimenter's left hand. This left hand JBS would persist past the sawing phase and would not be restricted to sawing-specific percepts or movements. That is, the participant's report of sensory states of her left hand (Experiments 1 & 2), or motor control of her left hand (Experiments 3 & 4), would show evidence of adaptation towards the left-hand state of the experimenter during the subsequent JBS-measurement phase.

In the first two experiments, immediately after sawing, buzzers were attached to the participant's left and right index fingers and thumbs. The experimenter held

her left hand—the one presumably integrated into the participant’s left-hand joint schema—next to an LED box, and aligned the index finger and thumb each to one of the LEDs. Across a number of trials, the participant received vibrotactile stimulation on one of her four fingers, and simultaneously perceived a flash next to one of the experimenter’s two left-hand fingers. The participant’s task was to locate the vibrotactile stimulation at their own fingers while ignoring the flash next to the experimenter’s fingers.

If the participant develops a JBS encompassing her left and the experimenter’s left hands during sawing, then stimuli near one of the experimenter’s left fingers would be readily and strongly mapped onto the participant’s own body schema, referencing a given location (i.e., a thumb, for example). If, in addition, the participant simultaneously perceives a buzz at an incongruent left finger (i.e., the left index finger), this should activate the corresponding location in her left hand schema. Thus, in those incongruent- finger trials (i.e., the participant’s left thumb buzz and the experimenter’s left index flash), the participants’ report of the buzz location should be impaired, in either speed, accuracy, or both. Conversely, if the buzz on the participant’s left hand and flash next to the experimenter’s left hand reference a homologous finger (i.e., either the participant’s and experimenter’s index or thumb), the participant’s dual activation of the corresponding representation in their left-hand schema should enhance localization responses. Figures 2 and 4 support both of these predictions through a comparison of the

inverse-efficiency of responses for left-hand trials in the solo and joint experimental conditions.

Inverse efficiency is a parsimonious measure of performance that scales the reaction time of a response (buzz localization in this case) by its accuracy. Higher scores on this measure indicate that an accurate response requires longer time to be attained. In both of Figures 2 and 4, it is clear that accurate localization of a left-hand buzz incurred more temporal cost on the Joint participant relative to the Solo participant when the concurrent flash referenced the partner's incongruent finger. Interestingly, the two figures also show that the temporal cost of accurate response was smaller for the Joint relative to the Solo participant when the concurrent flash referenced a homologous finger. Furthermore, Figures 3 and 5 show that this interaction is absent for buzz localization involving the participant's right hand, the hand that presumably does not develop a JBS. For the reader's convenience, a breakdown of the sample mean reaction time and accuracy comprising each of the four bars is included in the figures.

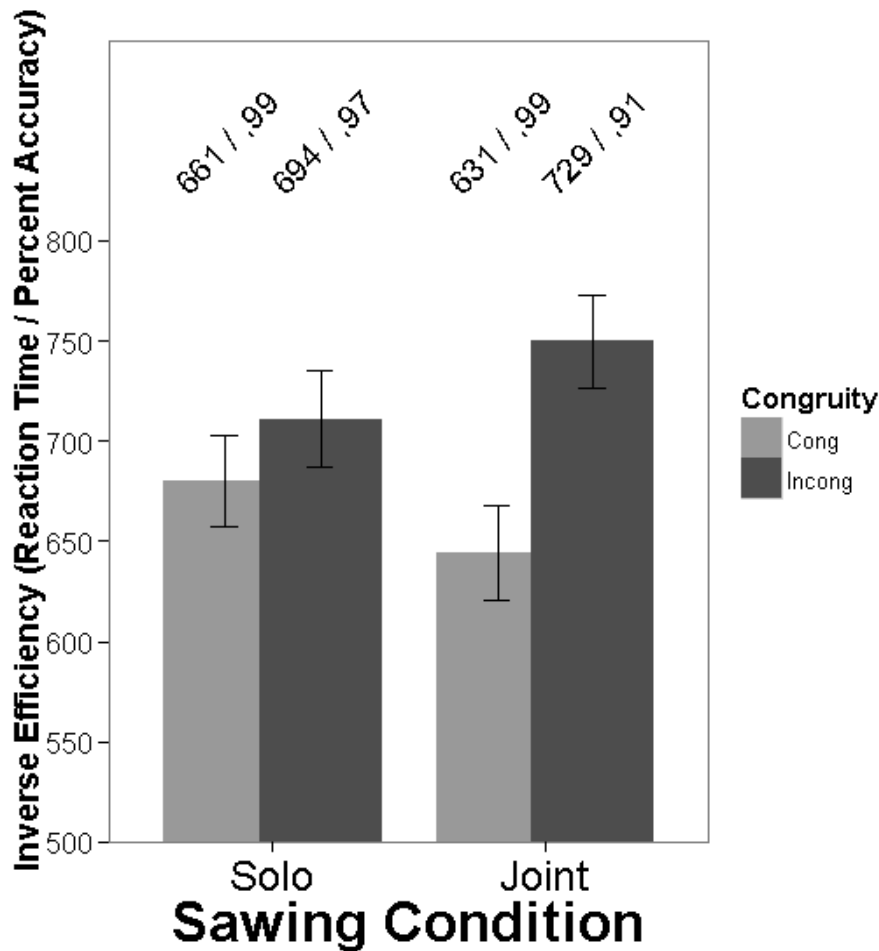


Figure 2. Data from Study 1 (Soliman et al., under review). Estimated inverse efficiency (IE) means of the participant's buzz localization on their left hand (presumably the one developing JBS) after either solo (left) or joint (right) candle sawing with a partner. After joint sawing, participants are significantly less efficient in buzz localization when their buzzed finger is incongruent with the concurrently flashed partner finger. They are significantly more efficient when the buzz and flash reference congruent fingers. The congruity by sawing condition interaction is statistically reliable. Sample reaction time / accuracy constitutive of inverse efficiency are printed on top of each bar.

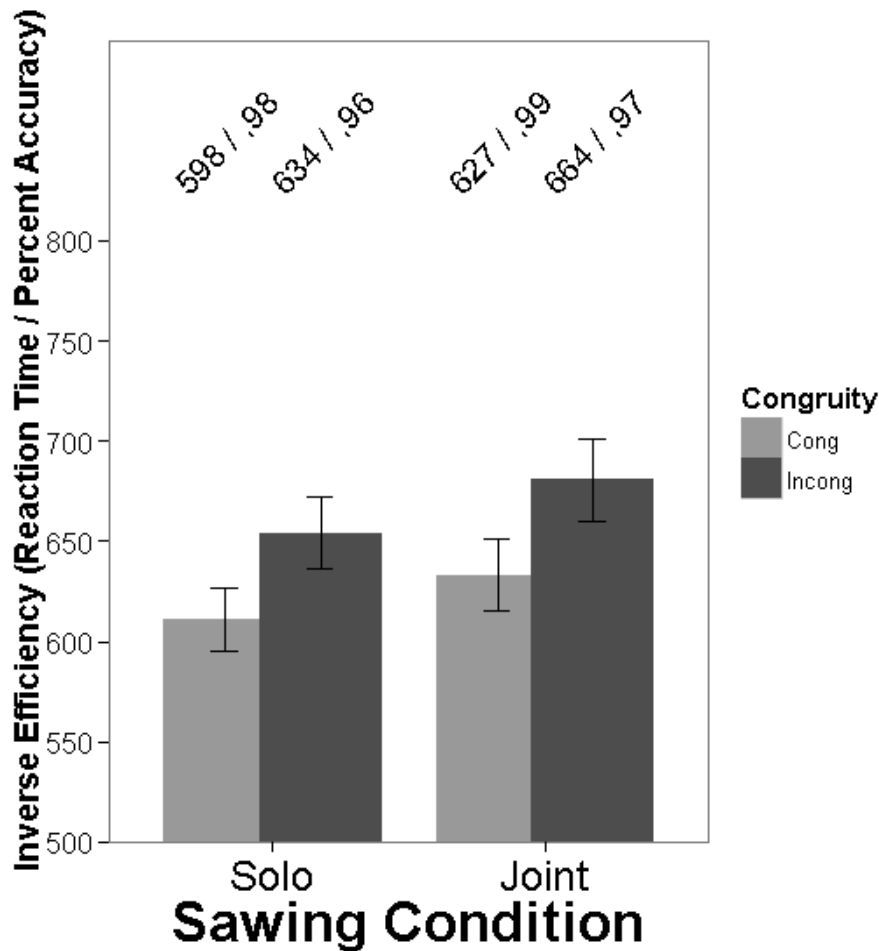


Figure 3. Data from Study 1 (Soliman et al., under review). Estimated inverse efficiency means of the participant's buzz localization on her right hand (presumably the one that does not develop JBS) after either solo (left) or joint (right) candle sawing with a partner. After joint sawing, participants are not significantly less efficient in buzz localization when their buzzed finger is incongruent with the concurrently flashed partner finger. They are not significantly more efficient when the buzz and flash reference congruent fingers. The congruity by sawing-condition interaction is statistically not reliable. Sample

reaction time / accuracy constitutive of inverse efficiency are printed on top of each bar.

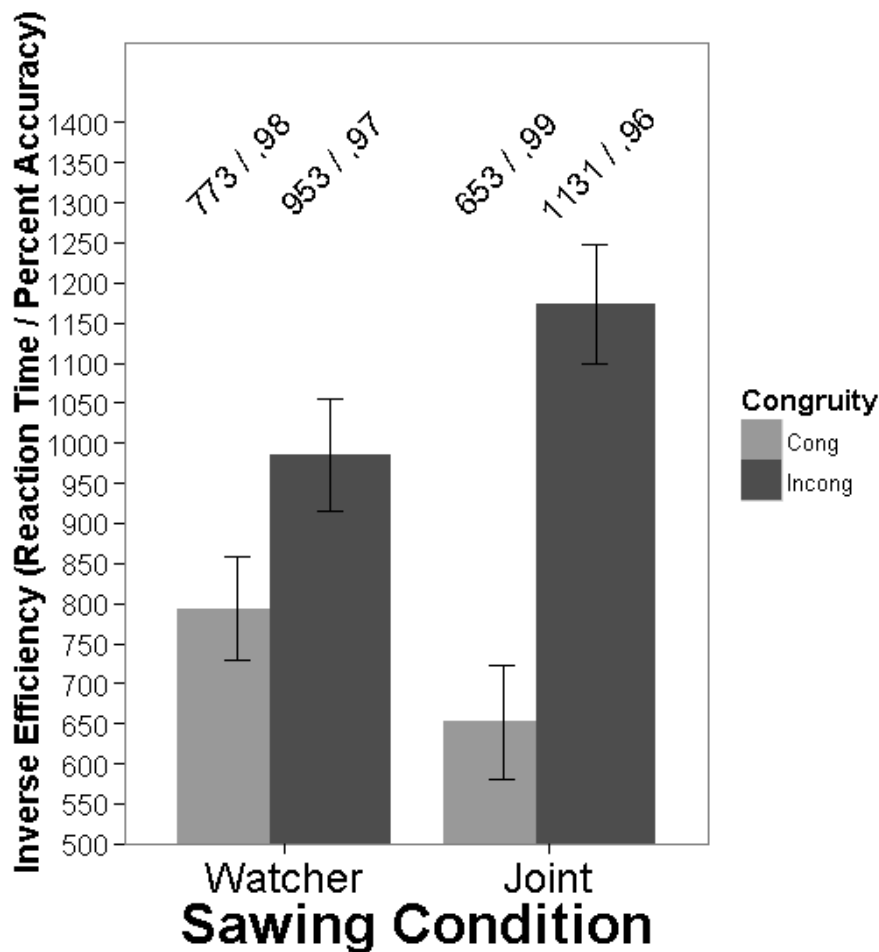


Figure 4. Data from Study 2 (Soliman et al., under review). Estimated inverse efficiency means of the participant's buzz localization on her left hand (presumably the one developing JBS) after either solo (left) or joint (right) candle sawing with a partner. After joint sawing, participants are significantly less efficient in buzz localization when their buzzed finger is incongruent with the concurrently flashed partner finger. They are significantly more efficient when the buzz and flash reference congruent fingers. The congruity by sawing condition

interaction is statistically reliable. Sample reaction time / accuracy constitutive of inverse efficiency are printed on top of each bar.

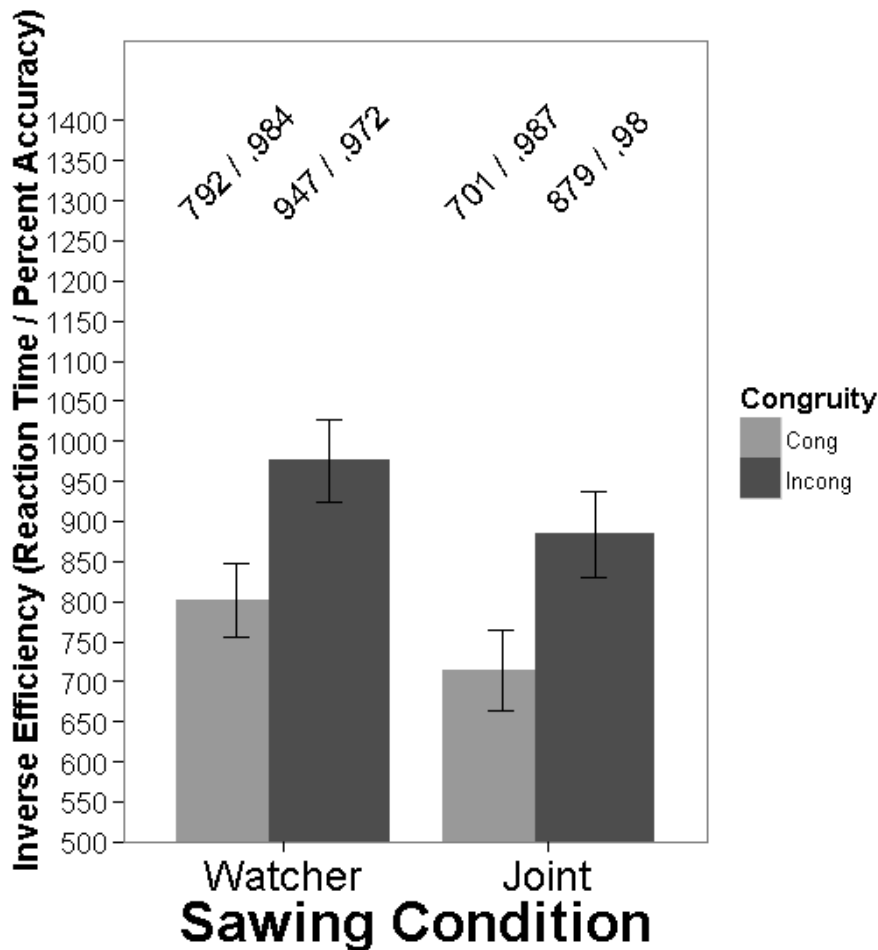


Figure 5. Data from Study 2 (Soliman et al., under review). Estimated inverse efficiency means of the participant's buzz localization on her right hand (presumably the one that does not develop JBS) after either solo (left) or joint (right) candle sawing with a partner. After joint sawing, participants are not significantly less efficient in buzz localization when their buzzed finger is incongruent with the concurrently flashed partner finger. They are not significantly more efficient when the buzz and flash reference congruent fingers.

The congruity by sawing-condition interaction is statistically not reliable. Sample reaction time / accuracy constitutive of inverse efficiency are printed on top of each bar.

In the second two studies, we examined if the JBS leads not only to multisensory spatial entanglement among the collaborating dyads, but also to an extended interpersonal motor resonance in a task that involves left-hand movement unlike that used during sawing. Before and after sawing, the participants were instructed to move a stylus in straight sagittal strokes using their left hand (the one that presumably develops the JBS) while watching their partner trace circles with her own left hand (the hand integrated into the participant's left-hand schema during sawing). If a JBS develops during sawing, then the perceived change in the position of the experimenter's left hand as she traces a circle would be strongly modeled by the participant's left-hand schema. As the participant's own motor system consults her own left-hand schema to program straight strokes, the circular trajectory instantiated there should bias the parameters of the programmed force. This should behaviorally be reflected in curvature of the attempted straight strokes, more so after than before sawing, and more so in the joint-sawing relative to solo-sawing condition. The results of two studies supported this prediction (see Soliman, Ferguson, Dexheimer, & Glenberg for data).

Thus, joint action leads to an extended spatial overlap between the representations of the task-relevant effectors of the co-acting dyad. This, in turn,

augments motor resonance in subsequent joint tasks that do not resemble, at both the conceptual or sensorimotor levels, the initial joint task. This task-neutral, temporally extended nature of the JBS lends itself readily to the potential for enhancing the mechanisms implicated during motor learning through imitative practice. As mentioned above, imitation has been shown to involve a kinesthetic and motor simulation during learning, and these are specifically the features that the JBS enhances. The empirical investigations of the present project were geared to examining the potential for an improved practice and learning outcome when the JBS and imitation are combined in one training regimen.

4. Research Question

Can the induction of a JBS among a trainer and a trainee enhance interpersonal sensorimotor coupling and learning during a subsequent imitative-practice session, in which the trainer repeatedly models a novel motor pattern using the JBS-relevant hand and the trainee concurrently imitates the pattern using her homologous hand?

4.1 Imitational Training

It is predicted that inducing a JBS between the left hands of a trainer and trainee through joint sawing will subsequently enhance the trainee's real-time imitation of the trainer, who will be modeling a novel motor pattern that does not resemble sawing. The JBS advantage is predicted to be reflected in the spatial dimension of the trainee's attempted imitation, such that the JBS participants' produced patterns will better resemble the patterns produced by the trainer. The JBS

advantage is also expected to be reflected in the temporal dimension of imitation, such that the imitating left hand of the JBS participants would be trailing closer behind the trainer's modeling hand. The JBS advantage will also be examined with a composite measure of performance efficiency that combines the spatial and temporal dimensions of the produced patterns (i.e., the temporal component scaled by the spatial component). It is predicted that the JBS will enhance the efficiency of imitation, such that the temporal cost of maintaining a performance that resembles the modeling pattern of the trainer will be less for participants who develop a JBS with the trainer's hand prior to imitation.

Statistically, the above should translate into a reliable main effect for the JBS manipulation (i.e., Joint or Solo candle sawing) on each of the above 3 measures of imitation. In addition, a main effect of time is predicted, such that all participants - with or without a JBS- should reliably improve on all 3 measures of imitation over the course of training. This is necessary to insure that the novel motor pattern is a) fairly adequately modeled by the trainer, b) is not too hard to impede improvement during practice, and c) not too easy to cause a premature ceiling effect.

Finally, it is tentatively predicted that the JBS will maintain its advantageous effect on the 3 measures of performance throughout the course of training (i.e., a null interaction between the above two factors). A reliable interaction, if present, is predicted to involve diverging rather than converging performance slopes, such

that the gap of performance widens over time between the (superior) performance of the JBS group and the No-JBS group.

4.2 Learning Outcome

It is predicted that the JBS will also lead to better learning outcomes as indicated by the quality of the participants free production of the novel pattern, unguided by the trainer's modeling hand. As above, the quality of the patterns freely produced by the participants will be gauged with spatial, temporal, and composite efficiency measures. The reference for these three measures will be the average pattern modeled by the trainer during the practice trials. In addition, a set of three equivalent measures will be computed to quantify the relation between the trainees' free performance and an ideal version of the pattern (see the methods section for details).

Statistically, the main effects of the JBS manipulation and of time on the two versions of the 3 measures are expected to be reliable. In addition, either a null, or a diverging-slope interaction pattern is predicted as above; the learning advantage of the JBS will be either stable or increase over time relative to the No-JBS condition.

4.3 Boundaries of the JBS Influence

Given the exploratory nature of the current study, it was necessary to investigate not only the proposed advantageous influences of the JBS on motor practice and learning, but to set the outer boundaries of the JBS effect as well. Accordingly, the novel pattern that the participants were required to learn was designed to

include two force components. One component was modeled by the trainer, while the other component was not (see the Methods Section for details). Accordingly, it was predicted that the JBS will have its advantageous influence on the magnitude and trajectory of learning selectively for the novel component modeled by the trainer. The other component should, from a theoretical standpoint, fall outside of the scope of the JBS influence. It constitutes a dimension of the learning problem that the trainees need to solve on their own; the solution cannot be found in the modeling behavior of the trainer. This force component should therefore be learned with a magnitude and trajectory equivalent in the group of learners who develops a JBS with the trainer and the group that does not. Statistically, this should manifest as a null effect for all main effects and interactions involving the JBS manipulation, and a reliable main effect for time.

CHAPTER 2

METHODS

This experiment examined if inducing a JBS between a trainer and trainee's left hands prior to imitative practice would lead to better acquisition of a novel left-hand movement pattern.

Forty-seven, right-handed, healthy participants were randomly assigned to either a control (n = 24) or an experimental condition. The design comprised three phases: a pre-test phase; a JBS manipulation phase; and a motor training phase. The procedures were identical for both of the control and experimental conditions except in the JBS manipulation phase. In this phase, participants in the experimental condition (hereafter termed Joint) were engaged in a 5-minute candle sawing task jointly with a trainer (a research assistant) to induce the hypothesized JBS between their left hands as in the previous experiments. In the control condition (hereafter termed Solo), participants were watched by a passive trainer as they performed an equivalent solo candle-sawing activity that presumably does not induce a JBS between the trainer's and participant's left hands.

Before the JBS manipulation phase, the Solo and Joint participants were familiarized with the apparatus and procedure of imitation practice in a pretest phase. The trainer used her left hand to model a unidimensional continuous movement pattern along the sagittal plane.

The pattern involved back-and-forth movement (arm flexion towards and extension away from the body) with variable speeds and reversal points, within a range of approximately 12 cm, and for a duration of approximately 4.2 seconds (see Figure 6). To guide the trainer through the pattern modeling task, a computer displayed a dot moving up and down the screen with the variable speed and direction reversals that define the pattern. The trainer held a wireless mouse with her left hand, and her task was to keep the mouse pointer on top of the moving dot throughout the pattern-modeling period. The participant had access only to the trainer's left-hand flexion-extension movements, and was instructed to hold his or her own wireless mouse and flex and extend their left arm to move the left hand along the sagittal plane in spatial and temporal synchrony with the trainer.

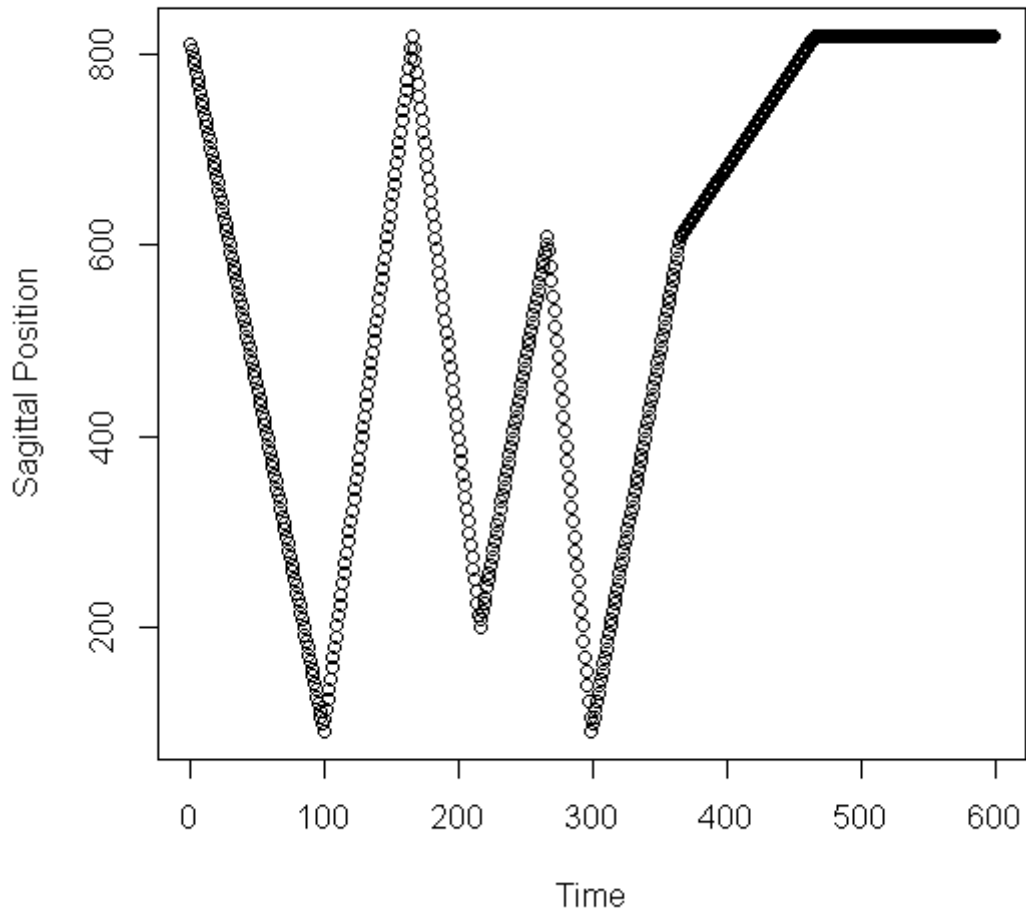


Figure 6. A time-series representation of the trajectory of the dot display on the computer monitor. The X axis represents time (600 increments, 7 milliseconds (ms) each, for a total duration of 4.2 sec). The Y axis represents movement of the dot along the vertical axis of the screen. The trainer moved her mouse along their sagittal plane to keep the pointer in contact with the dot through its trajectory.

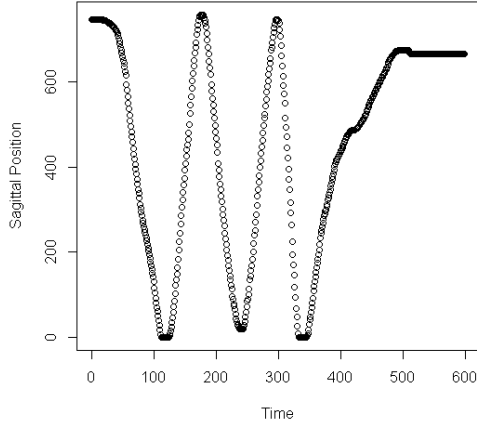


Figure 7. A time-series representation of the trajectory of hand flexion-extension of a participant's left hand during imitation practice. Time (in 7 ms increments) is on x axis and position along sagittal plane is on the y axis. Compared to the reference pattern in Fig 6, the attempted imitation here tends to preserve the spatial dimension of the pattern more than the temporal dimension.

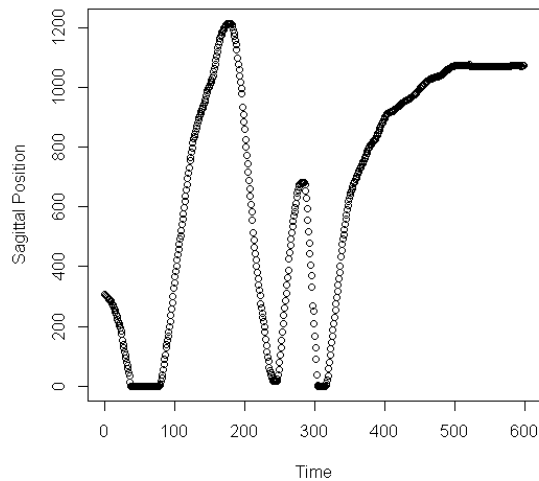


Figure 8. A time-series representation of the trajectory of hand flexion-extension of a participant's left hand during imitation practice. Time (in 7 ms increments) is on x axis and position along sagittal plane is on the y axis. Compared to the reference pattern in Fig 6, the attempted imitation here tends to preserve the temporal dimension of the pattern more than the spatial dimension.

To delimit the movement space for both the trainer and trainee, each were required to move their respective wireless mouse inside a wooden box (5 x 15 cm) lined with mouse pads. The boxes were fastened on a table top by Velcro strips approximately 30 cm away from the trainer's and participant's torsos. The pattern was modeled by the trainer (and imitated in real time by the participant) for three trials in this phase. The X and Y coordinates of the two wireless mice were recorded throughout the three trials.

After the sawing-manipulation phase, the trainer and the participant were engaged in the major phase of the experiment; the motor training and production

phase. This phase comprised three identical trial blocks, consisting each of three imitation-training trials followed by a free production trial (i.e., a total of 4 trials x 3 blocks). The procedures in the imitation training trials in this phase were similar to the imitation training trials of the pre-test phase. That is, the trainer held the wireless mouse with her left hand and moved it along the sagittal plane inside their wooden box to model the motor pattern, guided by a computer display of a dot moving with the speed and direction reversals characteristic of the target pattern. The participant imitated the modeled pattern in tandem, using his or her own left hand, mouse and wooden box. The pattern in this phase was more complex relative to the pre-test pattern, comprising more movement segments. Figure 6 is a time-series representation of the pattern. Figures 7 and 8 represent two imitative replications of the pattern attempted by different participants. Figure 7 illustrates a tendency towards spatial accuracy over temporal accuracy, while the reverse accuracy pattern is trending in Figure 8.

Importantly, a magnet was embedded in the right-hand-side wall of the box used by the participant during imitation practice trials. Another magnet was attached to the wireless mouse held by the participant during these trials. Together, the two magnets induced a repulsion force field, covering approximately the proximate 5 cm of the sagittal plane of movement inside the box. Given the orientation of the box, the participant's torso and left upper limb, the repulsion of the magnets induced a hand abduction force along the horizontal plane, pushing the hand leftwards and away from the participant's body.

The participants were made aware of the magnet and its force field, and were instructed to operate the mouse so as to avoid hitting any of the side walls of the box. They were therefore required to apply a hand adduction force to balance off the abduction force exerted by the magnet. Optimally, this adduction force was to be applied only in the proximate zone of the box covered by the magnet field. If applied indiscriminately along the entire (sagittal) range of motion, the mouse would hit the right-hand-side wall in the distal zone of the box, against instructions.

Importantly, no magnet was placed in the box used by the trainer to model the pattern. Thus, while the arm flexion-extension component of the novel pattern was modeled by the trainer and learned through imitation by the participant, the adaptation to the abduction-adduction force field was a force component experienced only by the participant and was to be learned through trial and error. After each set of 3 imitation-training trials, the participant was handed a magnet-free box, identical in all other respects to the training box. They received instructions to freely produce the pattern from memory, unguided by the trainer. Given the absence of the magnet, it was predicted that the participants would produce noticeable motor after effects along the horizontal plane. This should ideally cause over adduction of the hand in the proximate zone of the box (i.e., where the magnets had been placed during training). Thus, in the free production trials, the participant was to demonstrate learning of the flexion-extension force component of the target pattern (through accuracy of spatial and temporal

replication) and learning of the abduction-adduction component of the pattern (through motor after effects).

To sum up, the experiment involved a pretest phase comprised of 3 imitation training trials, then a JBS manipulation phase in which participants either developed or not a JBS encompassing their left, and the trainer's left, hands. Finally, all participants were run in interleaved training and free-production trial blocks. The pattern involved a force component designed to be learned through imitation (i.e., flexion-extension) and another force component that would ideally be learned through trial and error. Only the former component was predicted to be differentially influenced by the JBS manipulation.

CHAPTER 3

RESULTS

3.1 Computing the Dependent Variables

The raw data set included the X and Y coordinates of the wireless mice moved by the trainer and the participant during each of the 12 imitation practice trials (three in the Pretest Phase and 9 in the Training Phase after sawing). In addition, the participants' mouse coordinates were also recorded during the three free-production trials in which participant's attempted to produce the pattern without the trainer's guidance.

The duration of each trial was 4.2 seconds, and the mouse position was sampled every 7 ms. Accordingly, the hand movement trajectory of the participant and the trainer were independently represented by the X and Y coordinates of 600 points during any given trial. The Y coordinates represented hand movement along the sagittal plane (flexion and extension for both of the trainer and the participant). The x coordinates represented hand movement along the horizontal plane (hand adduction and abduction). Each of these set of coordinates was used for a different set of analyses.

3.1.1 Flexion-Extension Force Component

For each of the 12 imitation-training trials, a lagged cross correlation was run to compute the highest (positive) correlation coefficient that could be obtained between the Y coordinates of the participant's left-hand trajectory and the Y coordinates of the experimenter's left-hand trajectory. This resulted in a set of 12

cross-correlation coefficients (CCC) and their corresponding lag values for each of the 47 participants.

The Y coordinates representing the left-hand trajectory of the trainer during each set of three imitation practice trials were averaged. A lagged cross correlation was run between the average trajectory of the trainer's left hand movement in a given set of 3 training trials and the trajectory of the left-hand movement of the participant in the subsequent free-production trial. Thus, for each of the 47 participants, a set of three cross-correlation coefficients (CCC) and their corresponding lag values were obtained as indices of performance during the three free-production trials.

Given that the average trainer trajectory used above was expected to introduce significant noise to the CCC measure of learning, an additional measure of performance during the free production trials was computed. A lagged cross correlation was run between the y coordinates of the ideal pattern displayed on the monitor for the trainer (but not accessible to the participant) and the y coordinates of the left-hand trajectory produced by the participant in each of the three free-production trials. This produced an additional set of 3 free-production CCC's and their corresponding lag values. These were used as alternative indices of learning that were presumably less noisy relative to the above set of indices.

In total, the participant's degree of spatial and temporal synchrony with the flexion-extension component of the pattern (as modeled by the trainer) was

represented by a set of 18 correlation coefficients and their corresponding lag values. This set comprised three CCC's and lags for the three pretest imitation trials, 9 CCC's and lags for the 9 imitation practice trials, three CCC's and lags for the three free-production trials (i.e., participant-trainer), and an alternative set of 3 CCCs and lags for the free production trials (i.e., participant-pattern). This set constituted the DV that subsequent analyses were run on.

3.1.2 Abduction-Adduction Force Component

To quantify the proposed gradual adaptation to the abduction-adduction force field produced by the magnet, the x coordinates of the participant's left hand movement was recorded in two windows. The first window was centered at the magnet spot, with a dimension of 200 pixels along the sagittal plane, and 600 pixels centered horizontally on the longitudinal median of the floor of the box. That is, the center coordinates for this window was $x=300$ and $y=100$ pixels, aligned to the magnet spot of the box. For example, an average x-deviation score of 300 would suggest that the participant's hand-held mouse was, on average, on the longitudinal median of the box; a score of 100 indicates deviation to the left of the median line (i.e., away from the magnet side); and a score of 400 indicates deviation towards the magnet side of the box. A second, control, window with similar dimensions was centered at a "mirror" symmetric location at the distal end of the box.

For each participant, a total of 12 pairs of average deviation scores were computed (9 for each of the imitation-practice trials and 3 in the free production

trials). Each pair comprised a deviation score in the magnet spot and another in the no-magnet spot.

3.2 Random Assignment of Participants

The first preliminary analysis examined if participants randomly assigned to the Solo and Joint sawing conditions had equivalent motor performance prior to the sawing manipulation. Two independent multi-level models (MLM) were run to predict the CCC's of the trainer and the participant and the lag between the participant and trainer during the pre-test phase based on subsequent sawing manipulation (Joint, Solo), trial (1, 2, 3) and their interaction. The main effect of sawing condition was statistically unreliable in both of the CCC and lag models, respectively $F(1, 86) = 0, p > .9$ and $F(1, 85) = 0.2, p > .6$. The main effect of trial was statistically reliable in both of the CCC and lag models, respectively $F(2, 86) = 6.7, p < 0.002$ and $F(2, 85) = 3.6, p < .04$. The interaction effect of sawing condition and trial was not statistically reliable in either model, $F(2, 86) = 1.04, p = .5$ and $F(2, 85) = .32, p > .4$. These results show that participants' spatiotemporal coupling of their left hand movements with the left hand movement of the trainer was equivalent across the two sawing conditions prior to the sawing manipulation. The improvement across the three pretest trials indicates that learning had already begun during the pre-test phase, but its magnitude and rate was equivalent across the Joint and Solo participants.

3.3 Quality of Trainer's Pattern Modeling

The second preliminary analysis examined if the flexion-extension force component of the pattern was modeled equivalently by the trainer for both of the Joint and Solo participant groups. An MLM model was set to predict the CCC of the trainer and ideal pattern as a function of the Sawing Condition (Joint, Solo), Block (1, 2, 3), and their interaction. The effect of Sawing was not statistically reliable, $F(1, 272) = .12, p > .7$. The effect of Block was statistically reliable, $F(2, 89) = 3.8, p < .03$. The interaction of Sawing condition and Block was not reliable, $F(2, 272) = .13, p > .8$. As Figure 9 shows, the trainer's flexion-extension modeling movement became progressively more similar to the ideal pattern over the course of the three trial blocks. Importantly, this was true in both of the sawing conditions, thus ruling out the possibility of a confounding influence on the participants' flexion-extension output.

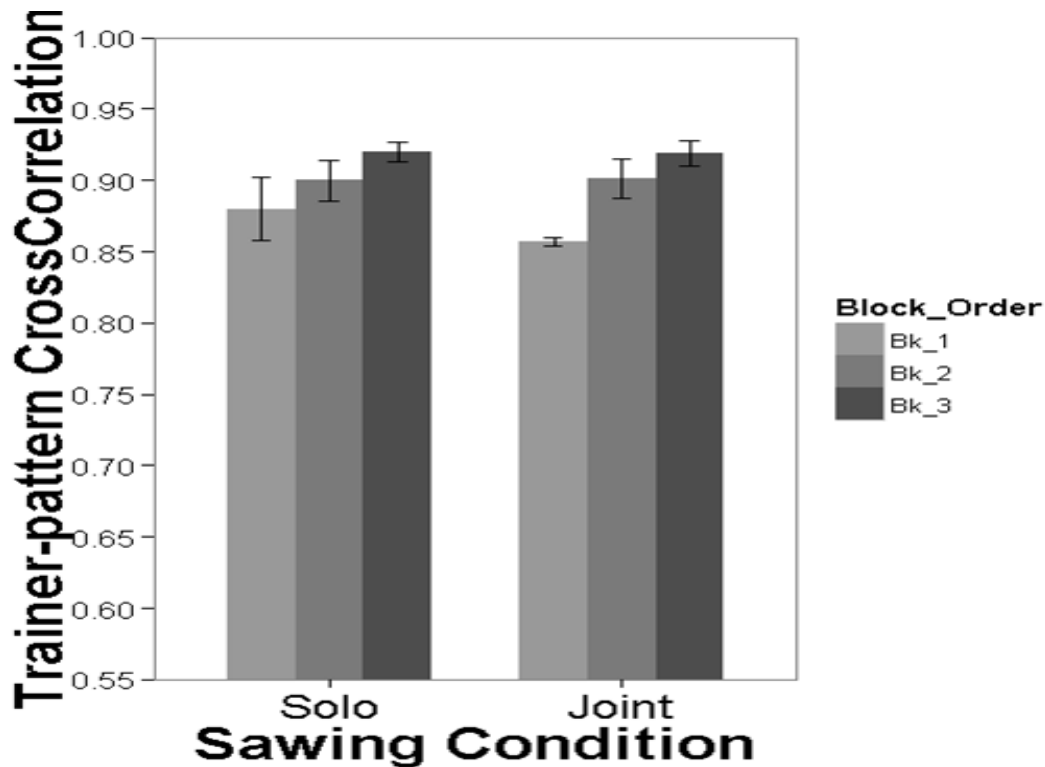


Figure 9. Estimated mean maximum cross correlation between the trainer’s left hand movement and the y coordinates of the ideal pattern during the three imitation trial blocks (bar colors). The trainer’s modeling improved over time, equivalently in the Solo (left) and Joint (right) conditions. Error bars represent one standard error of the mean.

3.4 Spatiotemporal Coupling of Participant and Trainer during Imitation Training

To examine the effect of the sawing manipulation on the participant’s ability to synchronize their imitative left-hand movement with the left-hand movement of the trainer, two independent MLM models were set to predict the CCC’s and the lags of the participant and the trainer during the 9 imitation training trials. The predictors in both models were the Sawing condition (Joint, Solo), the Block of trials (1, 2, 3), and their 2-way interaction. There were statistically reliable main

effects of the sawing manipulation on both of the CCC's and the lags, $F(1, 280) = 8.85, p < .003$ and $F(1, 280) = 8.4, p < .004$, respectively. There was a statistically reliable main effects of the order of trial blocks on the CCC's, $F(2, 90) = 6.6, p < .002$, but not on the lags, $F(2, 83) = 2, p = .1$. The interactions were not statistically reliable, $F(2, 253) = 1.2, p > .3$ and $F(2, 253) = 0.13, p > .13$. Figure 10 shows that, over the course of the three training trial blocks, both of the Solo and Joint participants demonstrate clear indications of learning. Their ability to synchronize the flexion-extension component of their left-hand imitative movement with the pattern as modeled by the trainer progressively improves from the first through the third block. There is a clear advantage for the Joint participant group that presumably developed a JBS with the trainer prior to training, however. This advantage is clear early on during the first block, and is maintained through the third block. Furthermore, the spatial synchrony advantage of the Joint participants does not come at the expense of temporal lag. The participants in the Joint condition were, on average, trailing at a shorter lag behind the trainer as they attempted to imitate their left hand movement, as shown in Figure (11).

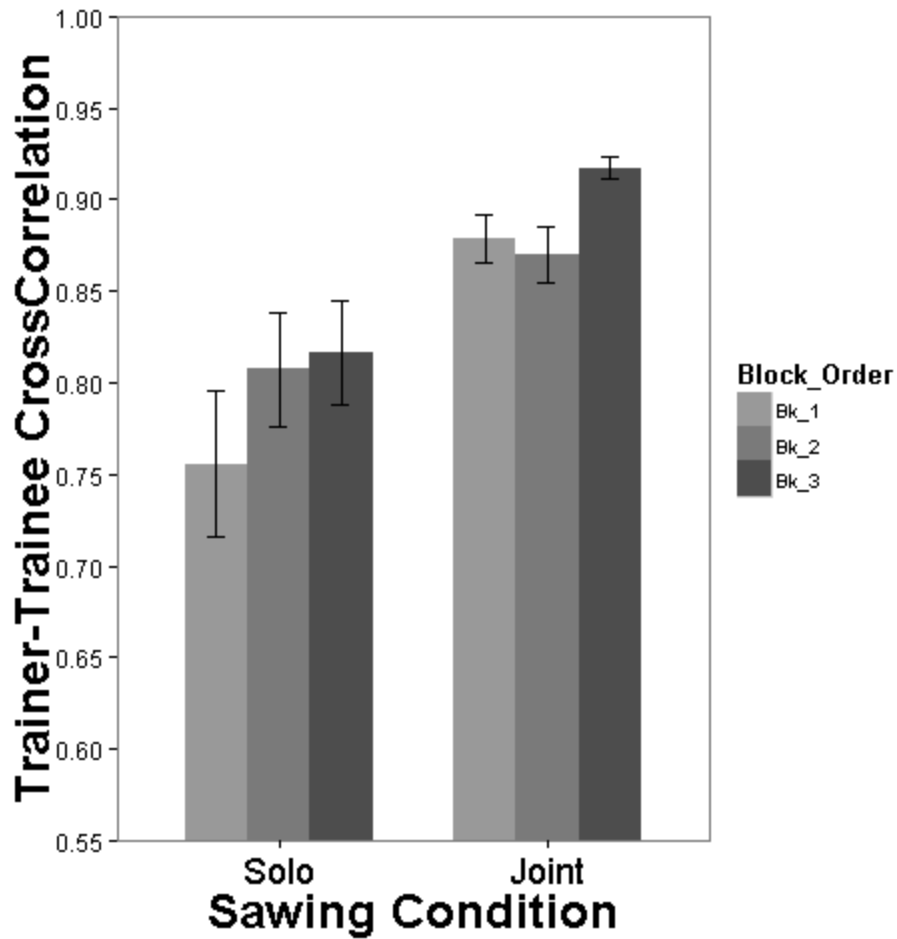


Figure 10. Estimated mean maximum cross correlation of the participant's and trainer's hand movement during the three imitation trial blocks (bar colors). The Joint participants (right) outperformed the Solo participants (left) in synchronizing their imitation movements with the trainer in all three blocks. Error bars represent one standard error of the mean.

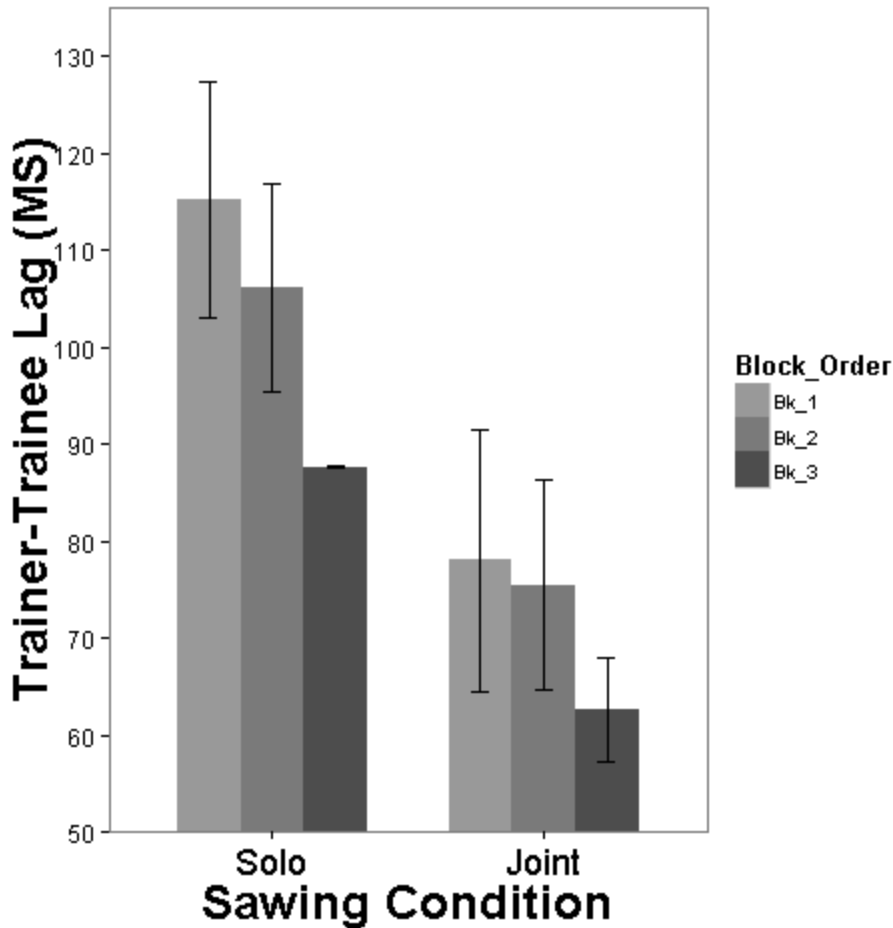


Figure 11. Estimated mean time lag of the participant’s imitation movement relative to the trainer’s modeling movement during the three imitation trial blocks (bar colors). The Joint participants (right) outperformed the Solo participants (left) in trailing closer behind the trainer during practice. Error bars represent one standard error of the mean.

To further investigate if the advantage of the Joint over the Solo participant reflects a strategic tradeoff between the spatial and temporal dimensions of the imitation performance, an inverse efficiency score was computed for each participant, in each trial. This composite score scales (i.e., divides) the value of

the trainer-participant lag in a given trial by the corresponding CCC obtained in the trial. The result is a measure of the temporal cost of performance per each unit of spatial accuracy. A higher score on this measure indicates that it was temporally costly for the participant to attain each additional unit of spatial correlation with the trainer.

An MLM model was run to predict the inverse efficiency scores by the Sawing manipulation (Joint, Solo), Block (1, 2, 3), and their two-way interaction. The effects of the Sawing manipulation and of Block order were statistically reliable, respectively $F(1, 280) = 10.2, p < .002$ and $F(2, 90) = 3.9, p < .024$. The interaction was not reliable, $F(2, 280) = .8, p > .44$. As Figure 12 shows, the temporal cost per unit of spatial accuracy of imitation dropped for all participants from the first to the third trial blocks. Throughout the training practice trials, however, it was consistently less costly for the Joint participants to attain imitation accuracy relative to the Solo participants.

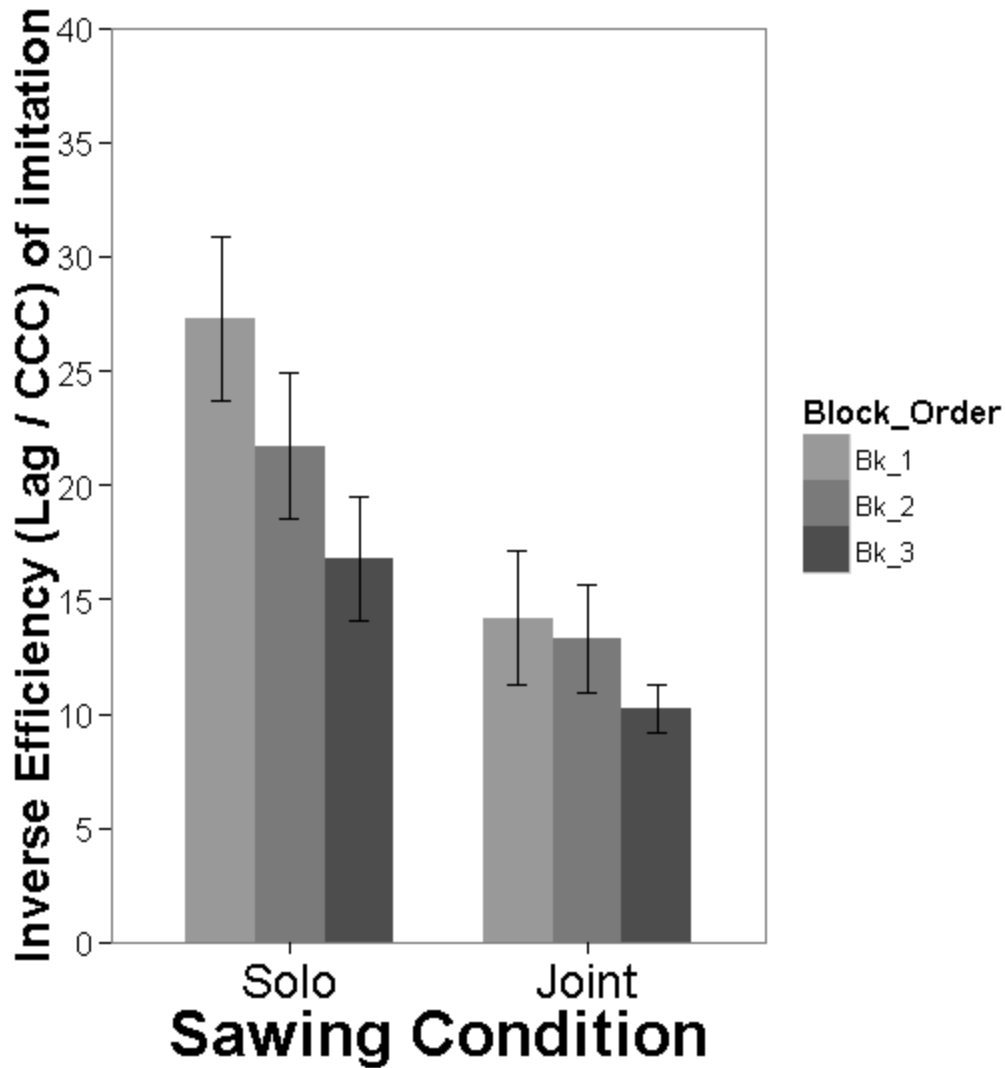


Figure 12. Estimated mean inverse efficiency score (lag in ms / ccc) of the participants' attempted imitation of the trainer's hand movement. Efficiency improved across blocks (bar colors) for all participants. Imitation performance of Joint participants (right) was consistently more efficient than the Solo participants (left) throughout. Error bars represent 1 standard error of mean.

3.5 Free Production

To examine the effect of sawing manipulation on the participants' ability to reproduce the pattern on their own, during the three free-production trials, two independent MLM models were run. In both, the independent variables were the Sawing condition (Joint, Solo), Trial (1, 2, 3), and their 2-way interaction. In the first model, the DV was the CCC's obtained between the flexion-extension trajectory of the left hand movement of the participant in a given free-production trial and the average flexion-extension trajectory of the experimenter's hand movement as they modeled the pattern during the preceding three imitation practice trials. In the second model, the DV was the lag at which this CCC was obtained.

In the lag model, none of the effects was statistically reliable. In the CCC model, only the main effect of the Sawing condition was statistically reliable, $F(1, 82) = 4.45, p < .038$. Figure 13 shows that participants in the Joint condition were better at freely producing a pattern that is more spatiotemporally synchronous with the average pattern modeled by the trainer during the preceding 3 imitation-training trials. This advantage was evident at the first free-production trial, and was maintained thereafter.

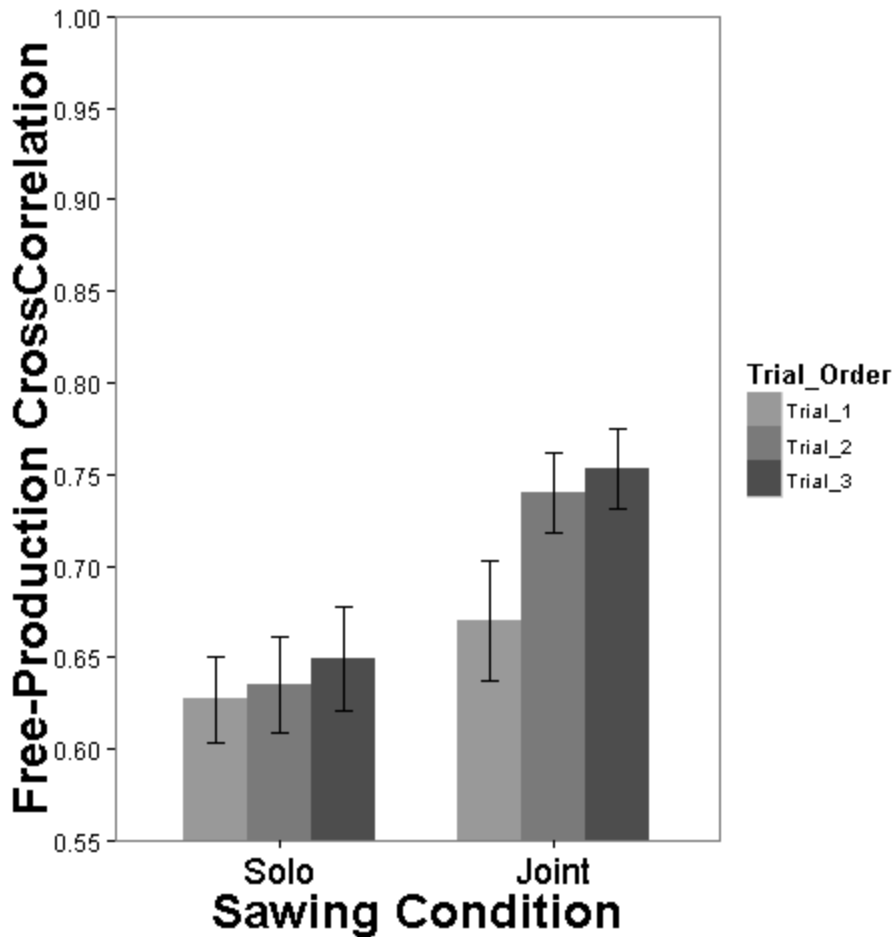


Figure 13. Estimated mean maximum cross correlation of the participant's hand movement during free production and the average trajectory of the trainer's hand movement in the preceding three imitation trials. Patterns produced by the Joint participants (right) better resembled the trainer's average pattern relative to the Solo participants (left). Error bars represent one standard error of the mean.

To obtain a measure of performance that simultaneously reflects the spatial and temporal dimensions of the participants' free production, an inverse efficiency score of the participants' hand flexion-extension trajectories was computed as above. An MLM model was run to predict the inverse efficiency scores by the

Sawing condition, Trial order, and their interaction. None of these effects were statistically reliable: $F(1, 82) = .8, p > .3$; $F(2, 82) = .7, p > .4$; $F(2, 82) = .9, p > .4$, respectively. This suggests that the temporal cost per unit of spatial accuracy was equivalent across the groups and did not improve over time.

The second round of analyses of the participants' performance during free production used the CCC and the corresponding lag values relating the participant's hand flexion-extension and the y coordinates of the ideal pattern.

Three independent MLM models were run with the CCC, the lags, and inverse efficiency scores as DVs, each using the Sawing condition, Trial order, and their two-way interaction as the IVs. None of the effects were reliable in any of the 3 models. The CCC model: $F(1, 87) = 1.5, p > .2$; $F(2, 87) = 1.5, p > .2$; $F(2, 87) = .4, p > .6$, respectively for the above effects. The lag model: $F(1, 87) = 1.6, p > .2$; $F(2, 87) = 2.7, p > .09$; $F(2, 87) = .16, p > .8$, respectively for the above effects. Inverse efficiency model: $F(2, 87) = 1.8, p > .18$; $F(2, 87) = 2.3, p > .1$; $F(2, 87) = .26, p > .7$, respectively for the above effects.

Figure 14 plots the CCC means estimated by the first model above. It is clear that the participants' flexion-extension output during free production resembled the spatial layout of the ideal pattern at a level that is numerically greater than zero and reliably different from it. However, the resemblance between the hand output and the pattern neither differed across the participant groups nor improved reliably over time.

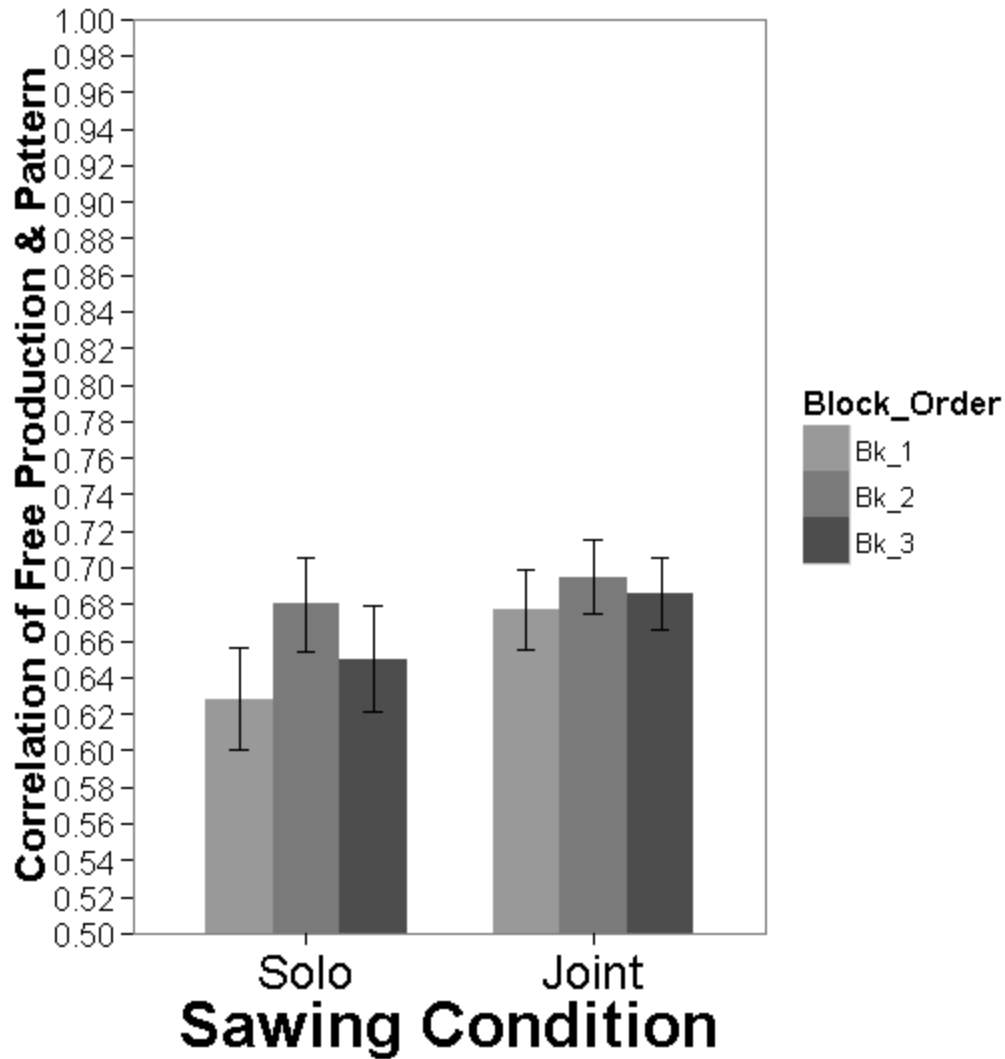


Figure 14. Estimated mean maximum cross correlation of the participant's left hand movement and the y coordinates of ideal pattern during the 3 free production trials (block colors). The patterns produced by the Solo (left) and Joint (right) participants were equivalent over time. Error bars represent one standard error of the mean.

3.6 Hand Adduction-Abduction during Imitation Training and Free Production

3.6.1 Adaptation to Abduction Force Field during Training

It was predicted that the participants would gradually adapt to the abduction-adduction force field introduced by the magnet over the course of the three blocks of imitation practice. It was also predicted that learning of this force component of the novel pattern would be equivalent across the sawing groups, given that it was not modeled by the trainer and was not subject to the advantageous influences of the JBS evident for the flexion-extension force component shown above. To examine these predictions, an MLM model was set up to predict the trainee's average left-hand deviation along the x axis of the box, as a function of the following factors and their two-way and three-way interactions: Box Zone (Magnet Zone, No-Magnet Zone), Block (1, 2, 3), and Sawing (Joint, Solo).

The main effect of the Sawing condition and all its interactions were statistically unreliable: Sawing $F(1, 729) = .4, p > .5$; Sawing x Zone $F(1, 729) = 1.03, p > .3$; Sawing x Block $F(2, 729) = .03, p > .9$; Sawing x Zone x Block $F(2, 729) = .5, p > 0.6$. The main effect of the Box Zone approached significance, $F(1, 729) = 2.7, p > .08$, and the main effect of Block order was significant, $F(2, 729) = 9.4, p < .0001$. But, most importantly, the interaction of Box Zone and Block order was statistically reliable, $F(2, 729) = 3.6, p < .029$.

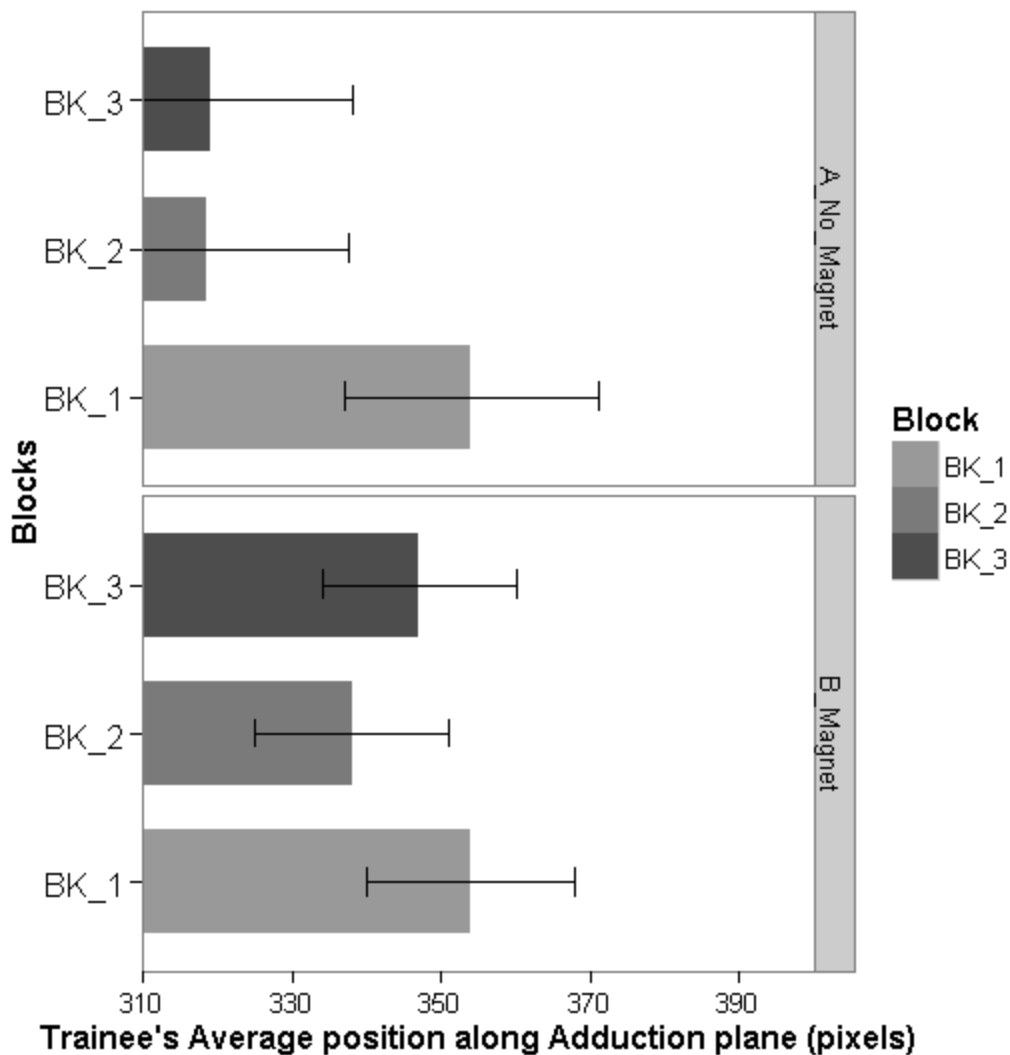


Figure 15. Estimated mean deviation of participants' hand along horizontal axis in the Magnet zone (lower panel) and No-Magnet Zone (upper panel) of the box. Bar colors represent imitation-trial blocks, collapsing over Sawing condition. All participants gradually adapt to the magnet force field by applying position-sensitive adduction force. Error bars represent 1 standard error of the mean. As shown in Figure 15, the participant's left hand was indiscriminately adducted in both of the Magnet Zone and the No-Magnet Zone during the first block of

trials. By the second block, the participants started to show zone-sensitive output of adduction force; more so in the Magnet zone than in the No-Magnet Zone. The third block of trials shows the clearest adaptation to the horizontal force gradient in the box: the participant's left hand is almost at the median of the box in the No-Magnet Zone, while significantly adducted to counteract the magnet repulsion in the Magnet Zone of the box. As predicted, this gradual adaptation proceeds equivalently regardless to whether the participant's left hand had developed a JBS with the trainer or not.

3.6.2 Adduction After-Effects during Free Production

To insure that the demonstrated adaptation to the adduction force component of the pattern during imitation training is indicative of updating of the parameters of the internal sensorimotor models, the magnets were removed during the free production trials. It was predicted that the participants' learned pattern of adduction force output would persist even in the absence of the magnets, leading to motor aftereffects along the adduction plane. To examine this prediction, an MLM model was set to predict the trainee's average left-hand deviation along the x axis of the box, as a function of the following factors and their two-way, three-way, and four-way interactions: Trial Type (Practice, Free Production), Box Zone (Magnet Zone, No-Magnet Zone), Block (1, 2, 3), and Sawing (Joint, Solo).

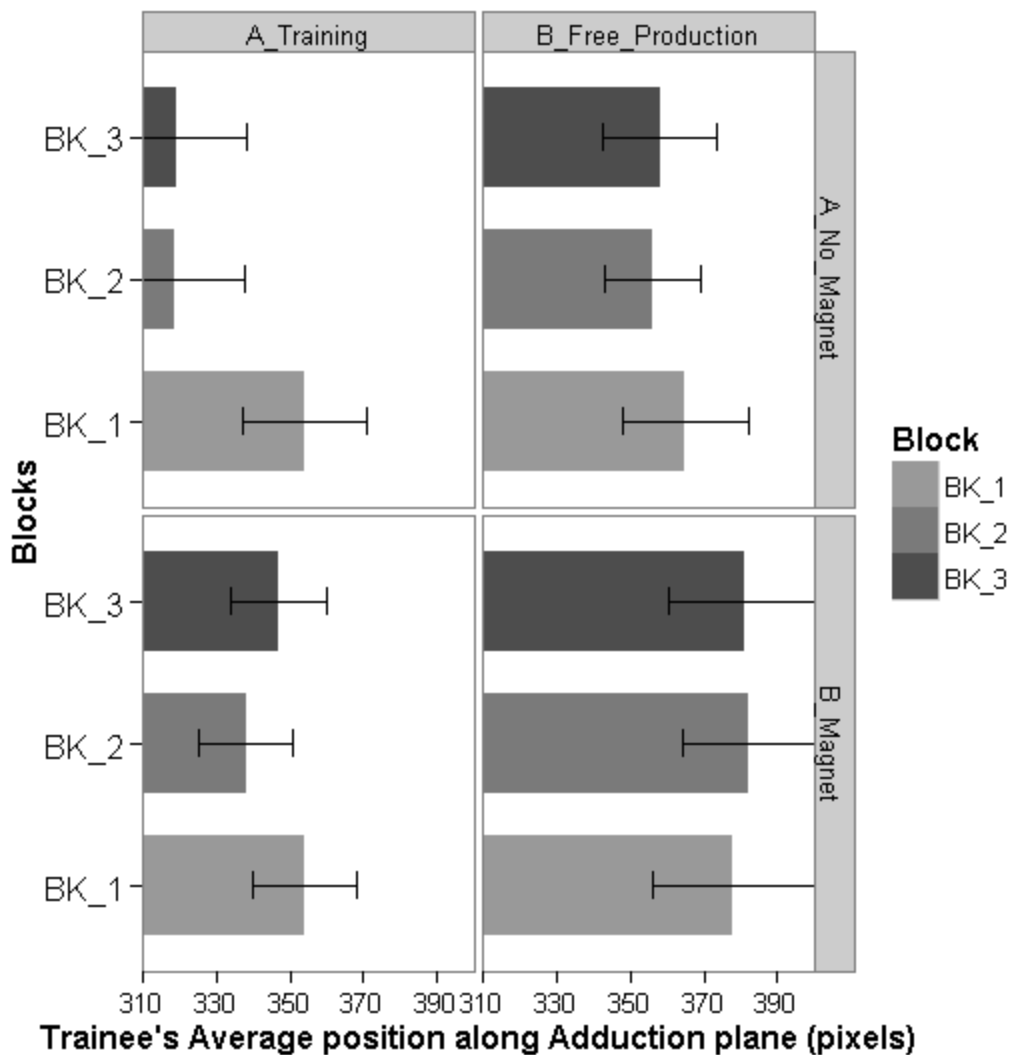


Figure 16. Average deviation along x axis for the participant's left hand in the training trials (left panels) and free production trials (right panels). Motor after effects shown in both the Magnet and No-Magnet zones after the magnet was removed in the free production trials (longer bars in the right panels).

As predicted, the main effect of the Sawing manipulation and all interactions it contributed to were statistically unreliable: Sawing $F(1, 469) = .33, p > .5$; Sawing x Block $F(2, 469) = 2.2, p > .1$.; Sawing x Box Zone $F(1, 469) = .7, p > .4$; Sawing

x Block x Trial Type $F(2, 469) = 2.2, p > .1$; Sawing x Block x Box Zone $F(2, 469) = 1.4, p > .2$; Sawing x Box Zone x Trial Type $F(1, 469) = .1, p > .7$; Sawing x Zone x Trial Type x Block $F(2, 469) = 2.3, p > .08$.

As predicted, the main effect of Trial Type was highly reliable $F(1, 469) = 10.4, p < .0015$. Unexpectedly, however, the two-way interaction of Trial Type and Box Zone was reliable $F(1, 469) = 16.8, p < .0001$ and the three-way interaction of Trial Type x Block x Box Zone was reliable $F(2, 469) = 3, p < .05$. These indicate that the difference in the deviation along the x axis between the Magnet and No-Magnet zone and the change in that difference over the course of the three trial blocks was not maintained in the free production trials as obtained in the imitation practice trials. Instead, as shown in Figure 16, there was a sweeping adduction aftereffects in the free production trials relative to the training trials (hence the main effect of Trial Type), but this over adduction was not selective to the Magnet Zone of the box nor did it gradually take shape over the course of the blocks (although, at least numerically, it is trending towards gradual diminution). Nonetheless, given that there were only 3 free-production trials (vs. 9 training trials), it could be argued that this crude after effect might need more practice to become position sensitive.

CHAPTER 4

DISCUSSION

Learning a novel motor skill involves the adjustment of the parameters of the sensorimotor system through practice. In imitation practice, the learner attempts to execute the target motor pattern while concurrently observing it being modeled by a skilled trainer. This practice mode has been shown by a number of neurophysiological and behavioral studies to promote better learning outcomes relative to passive observational practice or physical practice through trial and error.

In the present project, the aim was to explore if the motor-learning advantages of imitation practice could be further augmented through a supplementary technique derived from an on-going line of research in our laboratory. This work had already channeled converging behavioral evidence that joint dyadic action results in an extended sensory and motor representational overlap among the dyad members, termed the joint body schema (JBS). Co-actors in a task use the sensory and motor resources of their own bodies to covertly model the observed behavior of one-another to help coordinate during the joint task. Through neural adaptation, this automatic modeling, or resonance, does not cease as the initial task comes to an end. Rather, it continues leading to an incidental sensory and motor coupling that extends to subsequent novel tasks. Accordingly, it was hypothesized that having the participant develop a JBS with the trainer's relevant

effector through a familiar joint task prior to imitation practice on a novel motor pattern would enhance both the process and outcomes of training.

In the present study, participants either worked with their trainer to develop a JBS encompassing their left hands (Joint condition), or engaged in an equivalent solo activity while being watched by their passive trainer (Solo condition). After this JBS manipulation phase, all participants were run in an imitation practice schedule involving 9 trials of imitation practice where they attempted to copy the left hand movement of their trainer using their own left hand. In addition, participants were required to freely produce the pattern once after each set of 3 imitation trials. The participants and trainer all held wireless mice during training, and the trajectories of their left hand movements were recorded throughout.

Importantly, the novel pattern involved two force components. The arm flexion-extension force component required back-and-forth movement of the hand along the sagittal plane with variable speed and direction reversals at pre-specified points. A simultaneous hand abduction-adduction component involved adaptation to a force field along the horizontal plane. Only the movement along the sagittal plane was modeled by the trainer through the 9 practice trials, while the participant had to individually learn to adapt to the horizontal force field through trial and error.

The adaptation to the horizontal force field was included as a within-subject control condition to delimit the boundaries of the proposed influences of the JBS

on motor learning. It was found that, as predicted, participants in both the Joint and Solo conditions equivalently acquired the adduction force component. After an initial period of sweeping adduction of their hand, they ultimately learned to respond efficiently to the horizontal force gradient in the ambient environment. By the third block of practice, output of the adduction force was position sensitive; it was evident more so in locations where the participant needed to cancel off the abduction field exerted by the environment. The crude, position-insensitive adduction aftereffects evident in the free production trials show that the acquisition of the force parameters was far from perfect. Nonetheless, this manipulation served its intended purpose of demonstrating a predicted null effect of the JBS on the process and outcome of non-modeled motor learning.

As for the acquisition of the flexion-extension force component of the pattern, both of the Solo and Joint groups of participants showed a reliable improvement in the ability to synchronize their hand movement with their respective trainer across the 3 blocks of imitation practice. This main effect was important to confirm a number of design features. First, it confirms that the apparatus served its intended purpose. Second, it ascertains that the chosen motor pattern was neither too hard to learn nor too easy to cause an early ceiling effect. And, third, it assures that the use of cross-correlation coefficients as indices of performance (i.e., the dependent variable) was at least reasonable as it captured relevant components of the participants' and trainers' performance.

More importantly, the predictions of the JBS hypothesis were largely confirmed. Participants in the Joint condition consistently outperformed their Solo counterparts in synchronizing the movement of their left hands with the pattern as modeled by the trainer during practice. This was true of both the spatial component of their motor output (i.e., CCC) and in terms of the latency of their performance relative to the trainer's modeling movements (i.e., the corresponding lag values). A measure that captures the cost, in terms of interpersonal latency, for attaining spatial accuracy during imitation shows the advantageous influence of the JBS. Participants were more temporally efficient in attaining spatial synchrony if they had developed a JBS with the modeling hand of the trainer.

The relative advantage in terms of the three performance measures was evident at the first block of training trials, which indicates that its cause is antecedent to training: the development of the JBS. Moreover, judging from the statistical unreliability of the interaction between the sawing condition and order of blocks, it does not appear that the Solo participants were closing the performance gap over the course of the three blocks of imitation trials. This might suggest that the interpersonal representational overlap driving the advantageous status of the JBS participants is maintained through practice and does not taper off over time. The results of the free production trials indicate that the Joint participants developed better short-term memory traces of the pattern as modeled by the trainer relative to the Solo participants. The spatial component of their attempted

free production more strongly resembled the average pattern modeled by the trainer during the antecedent set of imitation trials. This privilege does not extend to the temporal dimension of free production, however. There is no reliable evidence that the participants in either group improved over time in terms of the latency of their replication of the pattern they perceived the trainer perform. Also, although there is evidence that the participants in both groups can produce the ideal pattern, there is no evidence that either the JBS or further practice can improve the spatial or temporal dimensions of their attempted free replication. This might suggest that either further practice or better performance measures are needed to detect learning effects, and possibly an effect of the JBS on learning.

The results of the free production trials are important in another, theoretical, sense. They might provide an indirect answer to the questions: What exactly did the Joint participants learn as a result of developing a JBS? Did they learn to better coordinate the movement of their hands with the movement of their trainer? Or did they develop, in addition, a better internal representation of the motor pattern?

An affirmative answer to the former question might predict that the Joint participants were at a greater disadvantage when they were required to freely produce the pattern, unguided by the hand they learned to couple their output to. On this assumption, thus, their performance should have a) dropped relative to the imitation practice trials and b) more so than the Solo participants. The former

is true, but is true of both the Joint and Solo participants, indicating that the JBS benefits are not limited to enhancing the learners' interpersonal coupling ability. Stronger evidence against this hypothesis is that the Joint participants still outperformed the Solo participants even when deprived from the coupling hand. This indicates that the benefits of the JBS are primarily in the development of better internal model of the motor pattern, presumably in terms of the force schedule required to produce it.

Overall, the present exploratory study has confirmed the hypothesized benefits on motor practice and learning of having the trainer and trainee perform an initial joint task involving interpersonal sensorimotor synchrony. Although the mechanism mediating these benefits was not directly examined, it could be indirectly inferred from previous studies on motor learning through imitation and on the JBS construct. The former literature points to the higher motor resonance effects of attempting to perform an action while perceiving it concurrently performed. The latter points to the possibility that an extended body-representation overlap could result from initial synchronous joint action. Combined, these mechanisms may indicate that the extended body overlap between the trainer and trainee's representations of the task-relevant effectors (i.e., JBS) led to an even higher motor resonance during training. This independently led to better spatiotemporal coupling during imitational practice and to the development of better short-memory traces of the practiced pattern.

A follow-up study is currently being run to directly examine this hypothesized mechanism. In this study, the design teases apart what needs to be performed from how it should be performed. That is, after either Joint or Solo sawing activity with a trainer, the trainer models the target pattern either by flexing and extending the left arm, or by abducting and adducting the arm. In both conditions, the participant imitates along through cycles of arm flexion and extension. And, in both conditions, the pattern modeled by the trainer runs along the sagittal plane from the participant's perspective. If, as has been assumed here, the JBS induces in the participant an extended representational overlap encompassing the relevant effector of the trainer, and if this augments incidental motor resonance with the perceived movements of the trainer, then the JBS should actually harm the Joint participants, relevant to the Solo participants, selectively when the dyad uses non-homologous muscle structures to produce the pattern. Alternatively, if, contrary to what had been assumed here, the JBS enhances interpersonal coupling at the perceptual spatial level, not at the muscular-resonance level, then the Joint participants should consistently outperform the Solo participants regardless to whether the trainer-trainee dyad uses homologous muscle structures to produce the same spatial layout of the pattern or not.

Future studies also need to examine the effectiveness of the hypothesized JBS-supplemented training regimen for more complex motor patterns, and with longer training schedules. Pending results from these studies, the proposed training

technique might bare substantial benefits for trainees of new motor skills, such as athletes, dancers, and surgical-procedure students. The technique could also enhance the feasibility of hemiparesis rehabilitation regimens that employ imitation as an essential component in their training schedule.

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