MECHANISMS OF IMITATION

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For My Family

Past, Present and Future
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Abstract

This thesis aims to discover the mechanisms of imitation by testing the predictions of three theories. These are Associative Sequence Learning Theory (Heyes and Ray, 2000), Ideomotor Theory (e.g. Prinz, 1997), and Active Intermodal Mapping (e.g. Meltzoff & Moore, 1997). Chapter 1 identifies three issues upon which the theories of imitation can be differentiated. The first is concerned with the development of effector-dependent representations through observation. The second and third relate to the role of awareness and experience in imitation. These differences form the basis of the experiments reported in Chapters 2, 3 and 4.

Experiments 1 – 3 (Chapter 2) investigated whether effector-dependent representations could be formed through action observation. A series of tests based on the serial reaction task (SRT) were utilised. It was found that with relatively short, simple movement sequences, participants learned the structure of the sequence as effector-dependent motor representations. Sequence knowledge could not be expressed using effectors other than those used by the observed model.

Experiments 4 – 6 (Chapter 3) used similar tests to those in Chapter 2 but investigated whether a longer, more complex, movement sequence could be learned implicitly i.e. without concurrent awareness. Two experiments suggested that observation of a movement sequence, but not inanimate stimuli, could support implicit learning.

Experiments 7 and 8 (Chapter 4) investigated the role of experience in imitation. It was shown that while responses made to movement stimuli were faster when stimulus and response movements matched, compared to when they were different, the advantage for matching movements disappeared after incompatible training. This result supports an experience-based, rather than innate, view of imitation.

The results of the experiments reported in this thesis suggest imitation is experience-based, supports effector-dependent learning by observation, and can operate without awareness. This combination is best described by Associative Sequence Learning Theory.
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Chapter 1: Introduction

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1.5 Summary
1.1 What Is Imitation?

The term imitation has been used to describe a number of reported behaviours in the literature on human learning. A common feature of all of these conceptualisations of imitation is that something is copied, and in the field of human movement imitation, that some aspect of a model's movement is copied by an observer of the movement.

Two defining features make movement imitation worthwhile for study, and distinguish imitative movement from action in response to inanimate external stimuli. These features can be seen in the following example. If one imagines a tennis coach demonstrating a serve to a novice, one realises that in order for the demonstration to be of any use, the visual representation of the coach's serve must be utilised in some way so as to produce motor commands which are the same as those performed by the coach. This is the first defining feature of imitative movement: motor commands are derived from perceptual representations. The foundation of the ability to produce matching motor commands from perceptual input is an issue of great theoretical debate.

The second defining feature is one of perspective. If the novice successfully imitates the coach's action the two actions will not 'match' from the novice's perspective. The novice will perceive the coach's actions as a whole body movement, albeit primarily of one arm moving in an overhead arc, while their own actions will be perceived as a movement of their arm and hand to hit the ball. Similarly, the coach may be able to tell that the novice's action matched the movement they had demonstrated, even though the visual information they received from their own movement and that of the novice differed greatly. For some kinds of imitative actions, movements will not
match from the perspective of either the model or the imitator, but only from a third-person perspective.

These two features of imitative movement have been described in the movement imitation literature as posing the ‘correspondence problem’ (Alissandrakis, Nehaniv, & Dautenhahn, 2002; Nehaniv and Dautenhahn, 2002). The correspondence problem occurs when matching motor output must be produced from perceptual information. Two seemingly incommensurate codes, one of patterns of stimulation received through the distal senses and the other of muscle contractions, must be made comparable. The problem is made more difficult when simple perceptual matching cannot be used, due to dissimilar perceptual feedback received from executing and observing the action. These ‘perceptually opaque’ actions (Heyes and Ray, 2000) are commonly whole body, or facial movements, which are not available for visual self-monitoring. These movements, when imitated, match from a third-person perspective but not from the perspective of either the imitator or the individual being imitated. Perceptually opaque actions are contrasted with ‘perceptually transparent’ actions in which feedback gained from action execution and observation is similar. Hand movements, for example, give rise to extremely similar visual percepts, if the orientation of the observer and model are matched.

In the literature on adult humans (but not in the developmental or comparative literatures), imitation is more commonly known as “observational learning” when the imitated movements were not previously part of the observer’s skill repertoire. This chapter reviews a number of studies which are described as experiments on observational learning of motor skills (e.g. Kelly and Burton 2001). These studies
investigate learning by imitation, or the imitation of novel movement sequences. Experiments are also presented in this chapter in which participants are not trying to imitate observed movements, and in some cases to perform the opposite movement (e.g. Brass, Bekkering & Prinz 2001). These experiments investigate the effect of action perception on the planning and performance of action and typically find that observation of an action primes the same movement in the observer. This finding is relevant to work on imitation; if an imitative action is prepared upon action perception then the correspondence problem has been solved, the observer needs only to execute the prepared movement to perform an imitative movement.

This review is concerned with three theories of imitation which attempt to solve the correspondence problem for both perceptually opaque and perceptually transparent actions. The theories are outlined in Section 1.2 and then evaluated in Sections 1.3 and 1.4. Section 1.3 focuses on two main points of agreement between the theories. The first relates to the formation of action representations from perceptual and motor representations (Section 1.3.1). The second is the common prediction that motor skills should be able to be learned through observation (Section 1.3.2). Section 1.4 considers three differences between the theories. These differences form the basis for the empirical work presented in chapters 2, 3 and 4. The main conclusions from the empirical work presented in this review are summarised in Section 1.5.
1.2 Theories of Imitation

Three theories of imitation shall be described, the Associative Sequence Learning model (Heyes and Ray 2000; Heyes, 2001, Section 1.2.1), Ideomotor Theory (e.g. Prinz 2002, 1997, Section 1.2.2), and the Active Intermodal Mapping model (e.g. Meltzoff & Moore 1977, 1994, 1997, Section 1.2.3).

1.2.1 The Associative Sequence Learning Model of Imitation

The Associative Sequence Learning (ASL) model posits that imitation is a result of general associative learning mechanisms. Associative theories of imitation prior to ASL can be split into those that assume that associations underlying imitative ability are formed through contiguous occurrence of stimuli and responses (e.g. Allport, 1924; Guthrie, 1935; Holt, 1931); and those that assume reward must follow presentation of stimulus and response for the two to become associated (e.g. Miller & Dollard, 1941; Skinner, 1953). Both types of theory are excluded from the present discussion of the correspondence problem as the theories either argue that the correspondence problem is never solved (by denying the possibility of novel imitation of perceptually opaque actions), or provide an insufficiently detailed description of key imitative mechanisms (e.g. Holt, 1931; see Heyes, 2000 for a review).

In contrast to these theories, ASL suggests that the correspondence problem is solved through bidirectional associations between perceptual and motor representations of an action. Perceptual representations are formed when another individual’s action is perceived and contain information received through the distal senses. Motor
representations contain motor commands needed to perform the action and somatosensory information received when the movement is performed (i.e. what it feels like to perform the action).

These associations, or excitatory links, produce co-activation of perceptual and motor representations of an action whenever either is activated. When the perceptual representation activates the associated motor representation, imitation becomes possible. The associations are formed in a Hebbian fashion when perceptual and motor representations are repeatedly activated at the same time. An increasing number of contiguous activations will lead to an increasingly strong association between the two representations. Associations formed through the co-activation of perceptual and motor representations are known as direct vertical links.

Associations between motor and perceptual representations ("vertical links") can also be formed indirectly when associations are separately formed between perceptual and motor action representations with a third representation. Through the common association, the perceptual representation becomes indirectly associated with the motor representation. The most obvious example of this process would be language. If an individual hears the word “kick” whenever they see someone perform a kicking action, the word “kick” will become associated with the perceptual representation of kicking. If the individual also hears the word kick when they perform a kicking action, the word “kick” will become associated with the motor representation of kicking. In this way the perceptual representation of a kicking action will be associated indirectly with the motor representation through the word “kick”. Co-activation of perceptual and motor representations through indirect vertical links.

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would quickly produce direct vertical links, i.e. activation of one representation would produce activation of the other without the necessity for intermediate phonetic or semantic activation.

Vertical links can explain the imitation of actions for which the individual already has perceptual and motor representations (i.e. the actions are familiar). To explain imitation of novel actions, Heyes and Ray (2000) invoke the idea that novel movements are composed of familiar movements, or movement primitives, arranged in a novel sequence. Observation of a novel movement sequence prompts two processes. The first is a perceptual process which decomposes novel action sequences into their constituent primitives. Horizontal links are formed between these perceptual primitives to form the representation of the overall sequence. The second process occurs when perceptual representations activate associated motor representations through vertical links. Motor representations will be activated in the same order and with the same temporal sequence as the perceptual representations. Activation of the motor representations will enable the observed novel movement sequence to be executed by the observer. The extent to which the executed act will be a faithful copy of the observed action will depend on the proportion of movement primitives that have associative links between their perceptual and motor representations.

The ASL model does not specify a system which compares perceptual and motor representations of matching movements. The individual does not have to ‘decide’ that representations are of the same action. It is possible for associative links to be formed between perceptual and motor representations which do not match from a third-person perspective. The reason why associations are more likely to be formed between
matching rather than non-matching movements is due to the environment. Heyes (in press) argues that activations are formed only when representations are activated contiguously, and that the environment of human development is constructed so that matching perceptual and motor action representations are more likely to be contiguously activated than non-matching representations.

Although it is more likely that non-matching movements will be performed at any time between two individuals, the range of possible non-imitative actions is so much larger than that of imitative actions. Thus, associations between specific non-matching actions are unlikely to be formed. Matching associations are more common due to the use of mirrors for example.

In summary, ASL suggests that imitation is accomplished through bidirectional associations between perceptual and motor action representations. These associations are formed when perceptual and motor representations are activated contiguously. Observation of an action leads to the activation of a perceptual representation. The associated motor representation is then also activated, and the action can be performed.

1.2.2 Ideomotor Theory

The ideomotor theory of imitation (e.g. Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Prinz, 1997, 2002) is based on Greenwald's (1970a; 1970b) extension of the ideomotor theory of action (James, 1890). James argued that, "Every representation of a movement awakens in some degree the actual
movement which is its object" (James, 1890, p. 1134); suggesting a model of action control in which the idea, or mental representation, of a movement is sufficient to cause its execution without any further need for volition. Greenwald extended this concept to include two central claims; that actions are mentally represented in terms of their perceptual effects, and that these effect representations are used to control action production (Greenwald, 1970a; 1970b. Prinz (1997) argued that ideomotor theory provides a useful framework to understand imitation as it demonstrates how action perception may prompt the production of a matching movement.

Ideomotor theory is distinguished from traditional models of perception and action in which perceptual and action codes are separate (e.g. Massaro, 1990; Sanders, 1980; Welford, 1968). Separate coding theories assume that sensory representations are fundamentally different from motor representations. The challenge for these theories is to specify the translation or transformation which enables a matching motor response to a perceptual event. Ideomotor theory, in specifying that perception and action share a common representational framework, does not need to specify a mechanism for translation of motor and perceptual representations.

Under ideomotor theory, actions are represented in terms of their sensory consequences, enabling information received through the senses to be matched to sensory consequences contained in action representations. Action representations can therefore be used to control action production by comparing expected sensory feedback with actual sensory feedback (see Wolpert & Kawato, 1998). The usefulness of this system with regard to imitation is obvious. Sensory consequences of a model's actions can be directly mapped onto a 'motor' representation which is coded in terms
of its sensory effects. This representation is then used to initiate and control imitative
behaviour in the observer.

A perceptual stimulus activates the action representation with which it exhibits the
most ideomotor similarity. Ideomotor similarity refers to the degree to which features
of a stimulus correspond to sensory features produced by particular actions. As
actions are represented in terms of their perceptual effects, perceptual input can be
compared directly with the action representation.

This process can be illustrated through imitation of a kicking movement. Visual
information received when a kicking action is observed will activate any action
representation with which it shares some degree of ideomotor similarity. The action
representation which exhibits the greatest degree of similarity will be activated most
strongly, and in the majority of cases this will be the ‘kicking’ action representation.
When an action representation is activated, the individual will perform the action
without the need for any further volition unless the action is actively inhibited.

Ideomotor similarity does not only arise as a result of simple, visual matching
between percepts and action effects. It can also arise as a result of high level cognitive
features. For example, tones and actions can exhibit ideomotor similarity, if they
share a common feature such as emanating from/being directed toward the same
region of space. This similarity may be based on the common effect of the tone and
the action to orient the individual’s attention to a particular region of space. Ideomotor
compatibility may also be based on symbolic features when a stimulus feature
symbolises an action. For example, if a high-pitched tone is produced in response to
hand opening, and a low-pitched tone in response to hand closing, then the respective
tones will share ideomotor similarity with the actions they represent. The tone is
included in the ideomotor representation as one of the action’s sensory consequences.

In summary, the ideomotor theory of imitation is based on the idea that there are
certain higher-level, late perceptual representations which share a common
representational system with early action goal representations. In this common
representational system, actions are represented in terms of their sensory
consequences. Under this system, perceptions of actions activate the action
representation which has the greatest degree of similarity in terms of expected sensory
consequences in the observer. The degree of similarity is not limited by low-level
spatial features, but is also influenced by higher-order cognitive effects.

1.2.3 Active Intermodal Mapping

The Active Intermodal Mapping (AIM) model (e.g. Meltzoff & Moore, 1977, 1983,
1994, 1997) introduces three theoretical concepts. The first, ‘organ identification’, is
the process by which infants come to identify parts of their body with parts of the
bodies of others. Meltzoff and Moore argue that this is the first step in the imitative
process. The second concept ‘organ relations’, refers to the capacity of the infant to
parse an observed action into a series of relationships between organs (parts) of the
body. The same capacity allows the infant to identify the organ relations of its own
body using proprioceptive feedback, and through organ identification, compare organ
relations of the model with its own organ relations. Organ relations provide a common
metric for the percept of an action to be related to the action of the perceiver. As perception and production are represented using the same coding system, mismatches can be detected between the present state of the observer and the state of the model. The third concept, ‘body babbling’, refers to the process of learning the relationship between muscle movements and the organ relations which result. It is argued that this process leads to the formation of a ‘directory’ of muscle movements and associated organ relations. After such experience-dependent learning, the infant will have the ability to produce muscle movements leading to specified organ relations.

These three processes provide the means for an imitative response to be made. Observed action is parsed into movements of the constituent body parts, (organ identification), which are represented as relationships between body parts (organ relations). Representations gained through action observation are stored and compared with the current state of the observer’s body (through organ identification based on proprioceptive feedback and encoded as organ relations) and any mismatch is detected. This mismatch becomes the organ relation target. The muscle movements needed to achieve this organ relation have been learned through body babbling and thus muscle movements can be specified which will reduce the discrepancy between the observed organ relations and those of the observer.

The model as it stands has not yet solved the correspondence problem. Although the infant can identify the organ relations of its own body, and can identify the organ relations of the model’s body, the two representations are still in incommensurate coding systems. Visual organ relations must still be compared to proprioceptive organ relations in order for a mismatch to be detected. According to AIM, the problem is
solved by the use of a supramodal representational system. This system encodes organ relations in a modality-general fashion. Visual and proprioceptive organ relations are translated into this common representational framework allowing them to be compared directly.

Meltzoff and Moore suggest that AIM explains infant imitation and forms the basis of adult imitative competency. The major developmental change in imitation occurs after a few weeks of life when perceived actions are no longer coded as organ relations, but rather goal-directed actions (organ relation transformations; Meltzoff & Moore 1997). The muscle movements required to perform the act and the supramodal representation of the act are integrated to become a single representation.

1.3 Points of theoretical agreement

The theories outlined above agree on two points. First, they all postulate that perceptual and motor representations are combined to produce action representations. Second, they all predict that it should be possible to learn motor skills through observation.

1.3.1 Action representations have both perceptual and motor properties

The three theories all state that imitation relies on the combination of perceptual and motor representations. Meltzoff and Moore’s AIM model argues that supramodal representations of actions, and the muscle movements needed to produce them,
become integrated into a single representation. Heyes and Ray’s ASL theory suggests that perceptual and motor representations become linked by bidirectional excitatory associations, and Prinz’s ideomotor theory argues that sensory inputs and motor outputs are both coded as perceptual representations of the effects of actions. The hypothesised combination of perceptual and motor representations is consistent with behavioural evidence that action perception 1) facilitates, and 2) is facilitated by action production. It is also supported by neurological evidence that action perception and production are associated with common patterns of 3) cortical, and 4) peripheral activation.

Researchers studying the behavioural link between perception and action production have concentrated their efforts into the question of whether perceiving an action influences its production. This is the direction of effect seen in imitation; an action is observed and responded to. However, in order to assess the claim that perceptual and motor representations become combined, it would be advantageous to demonstrate the opposite direction of effect i.e. that action production influences perception. If the direction of influence is only in one direction then two functional representations rather than one are implicated, as one representation with two sets of properties should always show co-activation of those properties.

1.3.1.1 The Influence of Action Perception on Action Production

Typically, studies which have demonstrated an effect of action perception on action production involve actions being performed in response to action stimuli. Participants are normally required to perform either a prespecified movement in response to all
stimuli (simple RT task), or asked to select an appropriate response based on a feature of the stimulus, e.g. colour, which is unrelated to the movement being performed (choice RT task). One of the stimulus actions matches that which the participant must use in response (compatible trials) and reaction times to matching stimuli are compared with non-matching stimuli (incompatible trials). A reaction time (RT) advantage on compatible trials implies that the perception of the action facilitated its performance by the observer.

An example of such a study is that of Brass et al. (2001). Participants were asked to lift (in one block), or lower (in another block) their index finger as soon as they saw movement of a stimulus hand. Irrespective of the stimulus movement, participants were always required to perform the same movement within a block. Stimulus movements were either compatible (matching), or incompatible (non-matching), with the response movement. Participants were faster to respond on compatible than incompatible trials. In order to discount an explanation of this effect in terms of movement direction alone, the same experiment was performed with the addition of stimuli which had been rotated 180°. Movement-type and movement-direction compatibility are unconfounded within these stimuli; movement was directed towards the bottom of the screen in a finger raise movement, and towards the top of the screen in a finger tap movement. Although compatibility due to movement direction was found, this was separate from, and significantly smaller than, compatibility due to movement type.

Brass et al (2001) provided evidence that perception could influence action which had already been prepared; perception affected when the response was made. Experiments
performed by the same group (Brass et al., 2000), showed that perception can also influence response selection, i.e. which response is made. Participants responded to one of two movement stimuli (raising or lowering of the index finger) with one of the same two movements. Response selection was not dependent on the observed stimulus movement, but on its colour. Colour of the stimulus movement varied from trial to trial, and therefore movement selection could not occur until after the stimulus had been processed. Although the movements shown were task irrelevant, responses made on compatible trials were faster than those on incompatible trials.

Using a procedure similar to that of Brass et al (2000), Sturmer, Aschersleben, & Prinz (2000) showed that static pictures representing end states of the two stimulus movements were as effective as the dynamic gestures in priming the compatible response. Similar results have also been reported by Craighero, Bello, Fadiga, & Rizzolatti (2002) using clockwise and anticlockwise wrist rotation as stimuli and responses, and by Kerzel & Bekkering, (2000) when participants were explicitly instructed to ignore the observed movement. In the latter study, the letters “Ba” or “Da” were presented to participants. Following the graphemic stimulus, mouth movements of a model articulating the sound “Da” or “Ba” were presented. This was the cue for participants to articulate the sound previously written on the screen while ignoring the mouth movements. Shorter RTs were found when the mouth movements and the response were compatible than when they were incompatible. This study, and those which have been presented in this section, provide compelling evidence that the perception of action influences action production.
1.3.1.2 The Influence of Action Production on Perception

If action representations contain perceptual and motor information, one would expect action to influence perception. Demonstrations of action-perception links have been provided by Ishimura and Shimojo (1994), Craighero, Fadiga, Rizzolatti, & Umilta (1999), and Wohlschlager (2000).

Ishimura and Shimojo (1994) presented bistable apparent motion patterns, which could give the impression of vertical or horizontal motion, to participants while they made occluded hand movements. The direction of the performed hand movements strongly affected the judged direction of the apparent motion presented in the visual displays. This result was replicated and extended by Wohlschlager (2000) who found that in addition to hand movements affecting perceptual judgement of visual displays, judgements were also affected by planned hand movements that were executed after the judgement had been made. In an experiment based on similar logic, Craighero, Fadiga, Rizzolatti and Umilta (1999) showed that preparing to grasp an object aligned with one of two orientations selectively facilitates perceptual identification of stimuli which correspond to the orientation of the prepared movement.

The forgoing experiments show immediate effects of action on perception. A series of experiments by Hecht, Vogt, & Prinz (2001) provided evidence of longer-term action-perception transfer. Participants completed both a motor test (producing timed sinusoidal arm movements), and a visual test (making timing judgements of visually presented sinusoidal movements), after training on just one of the tests. Test performance revealed both action-perception and perception-action transfer. Practice
of each single test led to better performance than controls (who received no training), on both types of test. Furthermore, no difference was found between motor and visual practice on either the motor or visual test.

Knoblich, Seigerschmidt, Flach, & Prinz (2002) argued that self-produced movements should be easier to perceive than the movements of others, due to a better match between the perceived movement and the perceiver’s motor plan. This result was obtained by Beardsworth & Buckner (1981) who presented subjects with point-light displays of their own walking movements, or those of their acquaintances. Despite greater visual experience of their acquaintances’ movements compared to their own, self-produced movements were more easily recognised.

Studies in Section 1.3.1.1 and 1.3.1.2 provide behavioural support for the combination of perceptual and motor representations. These studies show that perception of an action influences action production, and that action production influences perception. The studies in Section 1.3.1.3 and 1.3.1.4 assess whether action perception and production produce equivalent patterns of neural activity. Such equivalence would provide support for the argument that neural action representations have both perceptual and motor properties.

1.3.1.3 Equivalent Activation of Cortical Areas during Action Perception and Production

Many electrophysiological and functional imaging studies have shown related patterns of motor cortical activation during observation and execution of actions.
Areas which show similar patterns of activation include, the supplementary motor area (SMA), premotor cortex, primary motor cortex, cerebellum, parietal cortex and inferior frontal gyrus. This is true across a variety of methodologies including, functional Magnetic Resonance Imaging (fMRI) (Buccino et al., 2001; Decety et al., 1997; Manthey, Schubotz, & von Cramon, 2003), Positron Emission Tomography (PET) (Chaminade & Decety, 2001; Decety et al., 1997; Decety et al., 1994; Grezes & Costes, 1998; Grezes, Costes, & Decety, 1998, 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Ruby & Decety, 2001; Stevens, Fonlupt, Shiffrar, & Decety, 2000), Transcranial Magnetic Stimulation (TMS) (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), Magnetoencephalography (MEG) (Hari et al., 1998; Jarvelainen, Schurmann, Avikainen, & Hari, 2001), and Electroencephalography (EEG) (Babiloni et al., 2002; Cochin, Barthelemy, Roux, & Martineau, 1999). The equivalence between observation and execution holds at both the cortical level (e.g. Buccino et al., 2001; Grezes et al., 1998; Manthey et al., 2003), and when excitability is measured in peripheral neurons (e.g. Aziz-Zadeh et al., 2002; Fadiga et al., 1995; Strafella & Paus, 2000).

An experiment which suggests that activity seen in motor areas in response to action observation is specific to plausible biological action is that of Stevens et al (2000). Images of action stages were presented at two different speeds. At one speed the apparent motion induced by the image change was biologically plausible, and at the other speed the motion was biologically implausible. Biologically plausible motion produced activation in motor cortical areas but implausible motion did not.
In addition to demonstration of motor cortical activation during action observation, Iacoboni et al (2001; 1999) showed activation of perceptual areas of the cortex during action production. fMRI was used to identify areas of the cortex which are active during action execution and observation, but are maximally activated during situations where observed and executed actions match. One such area was the superior temporal sulcus (STS). The STS is a higher-order visual area which responds to biological motion (for review see Carey, Perrett, & Oram, 1997), and was found to be active during action observation as expected, but was also active during occluded hand movements.

1.3.1.4 Specific activation of cortical and peripheral neurons during action observation

The experiments reported above show general activation of motor cortical areas in response to action observation. Specific activation of neurons used to produce the observed act needs to be shown to provide support for the equivalence of perceptual and motor representations. While evidence for this level of specificity is not plentiful to date, an increasing level of specificity of motor activation through observation has been shown.

Studies which show specificity of motor activation using TMS are those of Aziz-Zadeh et al. (2002), Fadiga et al. (1995), Strafella & Paus (2000), and Maeda, Kleiner-Fisman, & Pascual-Leone (2002). These utilise a similar experimental logic. Participants observe a mixture of actions and non-actions. The actions observed differ in the muscles used to produce them. Motor Evoked Potentials (MEPs) are measured
from the corresponding muscles in the observer while TMS is applied to motor areas of the cortex. If action observation leads to activation of the specific areas of the motor cortex which control movements of the muscle being observed, then MEPs should be 1) greater for action observation than non-action observation, and 2) specific to the action being observed i.e. MEPs should only be greater during action observation for those muscles which would be recruited in performing the observed movement.

In their work of this kind, Aziz-Zadeh et al (2002) demonstrated a laterality effect. Larger MEPs were observed in the right hand when right rather than left hand actions were observed, while left hand MEPs only increased during observation of left hand movements. Greater specificity was shown by Fadiga et al (1995) and Strafella and Paus (2000). In both of these experiments, actions involving the right hand or the right arm were observed. When MEPs from arm and hand muscles were recorded, an increase in muscle excitability was found only upon observation of the action which required activity in that muscle. A recent study by Maeda et al (2002) indicated yet greater specificity. Participants watched one of three finger movements of the right hand, all performed by different muscles. MEPs recorded from the corresponding muscles in the participant’s own right hand were only higher when they observed a movement of that particular muscle.

Turning from peripheral to cortical activation, Buccino et al. (2001) used fMRI to measure activation caused by observing actions involving either the mouth, arm/hand, or foot. Activation caused by observation of the movements was centred on the part of the premotor cortex that is active when a person performs that movement.
Although action observation leads to the activation of motor cortical areas that would be used to perform the observed action, humans do not compulsively imitate. A potential mechanism for imitation inhibition has been described by Baldissera, Cavallari, Craighero, & Fadiga (2001). Spinal cord excitability was measured by eliciting the H-reflex in a finger flexor muscle while participants watched a hand opening or closing. The recorded H-reflex size varied according to the action observed in the opposite manner to that which occurs during execution of the movements. Baldissera et al posit that the inverted activation with respect to action execution seen at the spinal level may act to inhibit imitation.

1.3.2 Observational Learning of Motor Skills

In addition to implying a close relationship between action perception and production, all three theories of imitation predict learning of motor skills through observation. The ASL model of Heyes and Ray explicitly includes the learning of new motor skills through observation as a consequence of the imitation system. It is argued that novel skills can be decomposed into a sequence of motor primitives which are arranged in a novel combination or order. As long as these motor primitives have been previously learned by the observer (or have been specified innately), and vertical links between motor primitives and their perceptual representations have been formed through experience, novel actions can be learned through observation.

The AIM model of Meltzoff and Moore also includes the capability to learn motor skills through observation. Meltzoff and Moore specify an innate cognitive module
which transforms perceptual representations into supramodal representations which are used to produce actions. It is argued that the development of this module is not experience-dependent (e.g. Meltzoff and Moore 1997) and that imitation to some degree of fidelity can be accomplished on the first occasion that an act is perceived.

Ideomotor Theory claims that the common coding of perception and action enables observed actions to activate the action representation with which they share the most ideomotor similarity. If novel actions are composed of movement primitives, then observation of each primitive would activate the action representation with which it shares the greatest degree of ideomotor similarity and the novel sequence would be imitated.

Many studies provide evidence of skill learning by observation (see Weeks & Anderson, 2000, for details), and much of this literature has arisen from sports science. An example which claims to show facilitation of motor skill learning through observation is that conducted by Whiting, Bijlard, & Denbrinker (1987). Practice of a complex series of movements on a ski simulator was completed with or without simultaneous observation of an expert model. Practice supplemented by observation produced movements which were more fluent, and had a more consistent tempo, than practice alone. A problem with the claim that motor learning has taken place through observation is that participants observed the movement of the ski simulator as well as the model. It is possible that a perceptual representation of the ski simulator's movements, not of the model's actions, was used to guide performance.
Learning is less ambiguous in a study by Ishikura & Inomata (1995). Participants watched a model perform a sequence of balletic poses and reproduced these actions on test. As body movements were the only stimuli observed, the motor sequence was learned through observation of biological movement i.e. through imitation. This experiment provides good evidence that motor information can be learned through observation, a conclusion which is supported by the results of later experiments (Vinter & Perruchet, 2002; Weeks & Anderson, 2000).

A procedure which is ideally suited to discovering any observational learning of motor skills is the Serial Reaction Time (SRT) task (Nissen & Bullemer, 1987). The following section will present two studies which have investigated whether observation can support learning of motor skills, and have reached rather different conclusions (Kelly and Burton 2001, Heyes and Foster 2002).

Participants in an SRT task press an appropriate key in response to a stimulus appearing at one of a number of locations and their RT is measured. Stimulus location follows a repeating sequence over training trials but follows a different sequence or random order during test trials. An RT increase on test trials implies that the training sequence has been learned. This task can be easily adapted to investigate learning through observation by requiring participants to observe a model performing the task during training trials.

Kelly and Burton (2001, Experiment 1) compared the performance of practice participants (who respond during training), and observers (who watch practice participants during training) on an SRT task using a 12-item ambiguous sequence,
with 4 stimulus locations and four response alternatives. Each stimulus location is followed by more than one other in an ambiguous sequence, in contrast to unique sequences where the next stimulus can always be predicted by the current. No evidence of any sequence learning was found in observers when compared to practice participants.

In contrast, Heyes and Foster (2002) found evidence of observational learning using a 6-item unique sequence with six stimulus and response locations. The contrast between the results of Kelly and Burton (2001) and Heyes and Foster (2002) could be due to a number of factors. The most obvious difference between the experiments is the group used for comparison with the observers. Kelly and Burton (2001) compared sequence knowledge gained through observation to that gained through practice, whereas Heyes and Foster compared sequence knowledge of observers and practice participants to that of untrained controls (Dienes & Altmann, 2003; Perruchet & Reber, 2003). Thus Kelly and Burton cannot claim that observers did not learn through observation, rather that observers did not learn as much as those who practiced the task. A further difference between the studies is the competence of the model. Heyes and Foster used a highly practiced model who made very few errors. Kelly and Burton used a practice participant as the model; presumably this model produced more errors, slower response times and less fluid movements. Another major difference between the experiments is the sequence used. Kelly and Burton used a longer, more complex sequence than Heyes and Foster. It may be that only short simple sequences can be learned through observation. Thus, although Kelly and Burton (2001) did not find any evidence of observational learning, this evidence is not secure as it conflicts with the majority of findings in this area.
This section has presented empirical work demonstrating that information can be acquired through observation which aids motor performance. These experiments, in contrast to those presented in Section 1.4.1, do not elucidate the nature of the learning which takes place through observation. It will be argued below (sections 1.4.1 and 1.4.2), that the nature of the representations gained through observation is of theoretical importance for imitation research.

1.4 Theoretical Differences

This section discusses three issues which differentiate the theories of imitation described in Section 1.2, and evaluates existing empirical evidence relating to these issues. The three differences to be discussed are: the effector-dependence of motor representations formed through observation (Section 1.4.1), awareness of representations formed through observation (Section 1.4.2), and the origins of imitative competence (Section 1.4.3). These differences form the basis for the experiments reported in this thesis.

4.1 Effector-Dependence of Motor Representations Gained By Observation

Learning is said to be effector-dependent to the extent that training of one set of muscles (e.g. those of the right hand) does not generalize to another (e.g. those of the left hand). Effector-dependence of practice-based learning has been demonstrated in both monkeys (Rand, Hikosaka, Miyachi, Lu, & Miyashita, 1998) and humans (Bapi, Doya, & Harner, 2000; Marcovitch & Flanagan, in press). For example, Marcovitch
and Flanagan allowed human participants to learn a sequence of movements to spatial targets with one hand, and then tested performance of the other hand on the training sequence or a novel sequence. Performance of the training sequence was no better than that of a novel sequence, implying that sequence learning in the training phase had been effector-dependent.

The effector-dependence of motor representations formed through observation divides the three theories of imitation into two camps. AIM and Ideomotor theories both predict that representations gained through observation would not be effector-dependent, while the ASL model of imitation suggests that such representations may be formed through observation.

The ASL model of imitation predicts that under some circumstances, effector-dependent representations will be formed by action observation. These representations are formed when visual information activates motor representations directly, without intermediate symbolic or other higher-order representation. Thus, motor information can be learned without, for example, accompanying verbal script or perceptual representations. These observation-activated motor representations will be effector-dependent to the extent that prior visual experience of each movement component has been paired with activation of a distinct and constant muscle set. This condition is likely to be met for movements which provide visual feedback when they are executed, such as finger movements. When a person looks at their hands during manual movements, the sight of, for example, the left index finger lifting will be paired more reliably with activation of muscles in the left index finger than with activation of muscles in the left ring finger or the right index finger.
The AIM model of imitation would not predict that representations formed through observation would be effector-dependent. Although representations and information processing stages are underspecified by the AIM model, it is claimed that perceptual representations are transformed into 'supramodal' representations. Meltzoff and Moore (e.g. 1997) claim that supramodal representations can be translated into a variety of motor outputs, a feature incompatible with effector-dependence.

Ideomotor theory would also not predict effector-dependent representations, due to the many sources of ideomotor similarity between the perception of a movement and internal action representations. Movement percepts can bear ideomotor similarity to an action representation on spatial, visual, or even higher-level cognitive features. This feature of ideomotor action representations means that a perceived movement would activate a number of different action representations, any one of which could produce a 'matching' movement based on spatial, visual, or higher-order criteria.

For effector-dependent learning to be demonstrated through observation, motor representations, specific to the effector used by the model, must be formed. This was not demonstrated in the experiments presented in section 1.3.2, which indicated that information can be learned through observation which can aid motor performance, but did not demonstrate how it was encoded. Rather than motor representations, observers may form a perceptual representation ('mental movie') of the model's movements. Alternatively the movements of the model may be encoded in a symbolic or linguistic fashion. Empirical studies investigating the nature of representations formed through
observation of action are not plentiful; however those studies which have investigated
this issue are presented here.

An experiment using an instructed imitation procedure, ("Do what I do"), which
suggests that motor representations are not used in response production after
movement observation, is that of Bekkering, Wohlschlager, and Gattis (2000). Young
children (mean 4.4 years) imitated reaching movements to one of two targets which
followed either an ipsilateral or contralateral path. While children usually reached for
the correct target, they commonly used the ipsilateral hand when a contralateral
movement had been demonstrated.

Bekkering et al argued that these data show that young children focus on the goal of
the movement and perform the most familiar motor program associated with it, rather
than acquiring and implementing the observed motor program. This explanation was
supported by the finding that when the goal component was removed (by making
movements to one target rather than two), children successfully imitated the
movement path. If this explanation is correct, effector-dependent motor learning was
not shown, as action goals rather than movements were learned through observation.
However, it is possible that effector-dependent motor representations may have been
formed in Bekkering et al’s study, but task variables caused response to be based on
different action representations.

The only study to report effector-dependent learning by observation is that of Heyes
and Foster (2002). Observers watched an expert model train on the SRT task. On test,
observers demonstrated their sequence knowledge using the effectors they had
observed during training, but could not do so using different effectors. Thus Heyes and Foster claim to have shown the formation of effector-dependent motor representations through observation. This result is flawed however, as observers were given a chance to physically practice the training sequence prior to testing, and thus their sequence knowledge may have been acquired through practice and not observation.

The issue of whether effector-dependent motor representations are formed through observation is of great theoretical importance, yet is under-investigated in the literature on imitation. Chapters 2 and 3 of this thesis investigate whether observers can learn a sequence through observation of a model’s response using the SRT task, and more importantly, whether the knowledge they gain is effector-dependent (Chapter 2). If effector-dependent representations are demonstrated as a result of observational learning, doubt will be cast upon the processes of imitation specified by the AIM, and Ideomotor theories of imitation. Such a demonstration would however provide support for the ASL model of imitation which predicts that under appropriate conditions, (such as when movements are open to visual self-monitoring), effector-dependent representations will be formed by action observation.

1.4.2 The Role of Awareness in Imitation

Another major issue dividing the theories concerns the level of conscious awareness which accompanies imitation. This issue divides the AIM model from the ASL and Ideomotor theories of imitation. While ASL and Ideomotor theories suggest that under some circumstances imitation may occur automatically, without conscious
awareness (Heyes, in press; Prinz, in press), the AIM model posits that imitation is an active, effortful process, which is based on conscious representation (Meltzoff and Moore 1997). While the ASL and Ideomotor theories do not rule out the possibility that in some cases imitation is based on conscious processes, the AIM model of imitation cannot explain imitation which is automatic in nature, stressing as it does the role of effortful, goal-directed processing.

Consistent with AIM, previous research has generally concluded that observational sequence learning is only possible when participants have explicit knowledge of the sequence (e.g. Kelly, Burton, Riedel and Lynch 2003, Kelly and Burton 2001, Willingham 1999, Berry 1991), and is therefore fundamentally different from the implicit learning (“learning which proceeds without concurrent awareness of what is being learned.” Shanks & St-John, 1994), shown by practice participants in the SRT task (e.g. Seger, 1997; Willingham et al., 1989).

Kelly and Burton (2001) have argued that observational sequence learning is only possible when sequence knowledge is explicit. This hypothesis was supported by Kelly, Burton, Riedel and Lynch (2003) who compared observers of screen stimuli (but not of a model’s responses), with practice participants on the SRT task. In an attempt to manipulate the amount of explicit sequence knowledge, half of the participants in each group were shown the sequence as normal, and the other half were shown the sequence broken up into triplets through the use of colour (salient condition). The use of colour increased the amount of explicit knowledge gained by participants. Both practice groups, but only the salient observer group, showed significant sequence learning upon test. This provides support for the hypothesis that
practice participants, but not observers, are able to learn without explicit knowledge of the sequence.

The results of several studies are consistent with Kelly and Burton’s hypothesis, as they show the importance of explicit knowledge for observational sequence learning. Howard, Mutter, & Howard (1992) compared a screen-stimuli observation group and a practice group on the SRT task and a free generation task. During a free generation task participants are asked to generate the sequence upon which they have been trained in the absence of any cuing stimuli. Observers showed as much knowledge as practice participants on the SRT task and their knowledge was explicit as indicated by successful generation of the training sequence. Willingham (1999b) replicated this result and found that observational learning was only shown by those participants with high levels of explicit knowledge.

In contrast to the above findings, Seger (1997) found that ratings of familiarity and SRT performance were uncorrelated for screen-stimulus observers classified as having low explicit knowledge from a verbal report style questionnaire, i.e. participants were unaware of their sequence knowledge. Thus, Seger (1997) has shown implicit observational learning, at least on a subset of participants who had previously been classified as having low explicit knowledge. Seger’s evidence is questionable however, as it is in opposition to results obtained from many experiments which suggest that observational learning relies on explicit knowledge (e.g. Kelly et al 2003, Willingham 1999, Howard, Mutter and Howard 1992). It should be noted that observers in these experiments watched screen stimuli only. This
can be contrasted with the SRT experiments presented in Section 1.3.2, in which observers watched a model’s responses in addition to screen stimuli.

Turning from observational learning to imitation of behaviour, several studies suggest that social interaction may produce imitation which is unconscious and unintentional (e.g. Chartrand and Bargh, 1999; and Lakin and Chartrand, 2003). Participants in these studies are generally asked to freely interact with another individual whom they believe is a participant, but who is actually a confederate of the researchers. The confederate exhibits a target behaviour during the interaction (such as tapping their foot), and the tendency of the participant to perform the target behaviour during the interaction is compared to a baseline period when the participant is alone. Results consistently show an increase in performance of the target behaviour by the participant during the interaction. Also, during post-test debriefing, participants report that they did not notice the target behaviour being demonstrated, that they had no intention to imitate the behaviour, and that they were unaware of doing so. Thus, if one accepts the finding of these studies, it has been demonstrated that imitation can occur automatically, without conscious awareness or effort.

Such a conclusion would not be consistent with the characterisation of imitation suggested by AIM. However, the use of verbal report measures as tests of awareness has been criticised by Shanks and St John (1994). They argue that three features of a verbal report measure make it unsuitable for testing awareness. The first is the assumption that knowledge demonstrated at the time of verbal report is an accurate reflection of knowledge at the time of testing. It is possible that participants may forget information in the interval between the test of performance and their verbal
report. The second refers to a potential mismatch between the information upon which performance is based, and information asked for by the experimenter or which is able to be expressed verbally by the participant ('Information Criterion'). The third feature of a verbal report measure which makes it unsatisfactory as a measure of awareness is that it is likely that the verbal report measure and the test of production are differentially sensitive to conscious knowledge ('Sensitivity Criterion').

The AIM model suggests that imitation occurs only as a product of effortful goal-directed processing. In support of this position, several researchers argue that observational learning is only possible when information is explicitly represented. In contrast, both the ASL and Ideomotor theories of imitation suggest that automatic imitation, which does not need to be driven by conscious representations, can occur. Research using an insufficiently rigorous test of awareness suggests, but does not provide firm evidence, that unconscious unintentional imitation may be possible. The experiments reported in Chapter 2 of this thesis (experiments 4-6) investigated how aware participants are of information gained through observation of a model’s responses and/or screen stimuli in an SRT task. Evidence of implicit observational learning would support the ASL and Ideomotor theories but not the AIM model of imitation.
1.4.3 The Role of Experience in Imitation

Whether the ability to imitate arises from experience, or is present from birth, has direct relevance to theories of imitation. The two views can be mapped directly onto the ASL and Ideomotor theories, and the AIM model, respectively. The ASL model posits that imitative ability arises from contiguous experience of perceiving and producing action. Such experience causes vertical links to be formed between perceptual and motor representations which enable an imitative movement to be made. Thus, the range of movements that can be imitated by an individual is limited by the extent to which vertical links have been formed between perceptual and motor representations. Similarly, Ideomotor Theory holds that for an action to be imitated, the perceptual effects of producing the movement must be learned through experience. The perceptual effects of producing the movement become the action representation which is then used to imitate. Both ASL and Ideomotor Theory suggest imitative competence is a function of the individual’s experience of action perception and production.

Conversely, the AIM model argues that imitation is achieved through a dedicated, innate, cognitive module. This module transforms perceptual representations of action into supramodal representations which are used to produce matching motor output. The principal evidence in support of this view comes from studies of facial gesture imitation in newborn infants (‘neonates’). A wide range of laboratories claim to have demonstrated neonatal imitation (e.g. Field, Goldstein, Vaga-Lahr, & Porter, 1986; Field et al., 1983; Meltzoff & Moore, 1977, 1983, 1994), while several studies suggest that the evidence for neonatal imitation is flawed, inconclusive, or limited to
one gesture only (e.g. Anisfeld 1991, 1996, 2001, in press, Couturier-Fagan 1996). Such a limitation would suggest that infants do not imitate actions; rather that tongue protrusion may act as 'an innate releasing mechanism' (Heimann & Ullstadius, 1999), or that tongue protrusion may be an arousal response (Jones, 1996, in press).

Although such widely different views are held, there is little direct discourse between proponents of the opposite views (Heimann, 2002; Nadel & Butterworth, 1999), and therefore it is not possible to form a firm conclusion as to the existence and/or extent of neonatal imitation.

Although the results of neonatal research are equivocal, two recent studies with adult participants provided some evidence that experience plays a role in imitation (Howard et al., 2001; Maeda et al., 2002). Howard et al (2001) used fMRI to investigate neurological activation in the motor cortices of musicians and non-musicians upon observation of musically significant and non-significant movements. Greater activity was observed in musicians in response to observation of both types of movement. This may have been due to musicians' greater experience of performing imitative movements during musical training. More direct evidence of the importance of experience in imitation was provided by Maeda et al (2002). MEPs induced by TMS were recorded from thumb and finger muscles during observation of thumb and finger movements. As expected (see Section 1.3.1 above), MEPs were significantly larger from rest in each of the muscles only when movements were observed which involved the corresponding muscle. Additionally, movements were observed either in a familiar plane or rotated so as to appear unfamiliar. MEPs were significantly greater when movements were observed from the familiar angle, suggesting that the
activation produced during observation depended on the observer’s experience of the movement.

Turning from empirical data to artificial simulations of imitation, the studies of Alissandrakis et al. (2002), and Hoppitt & Laland (2002) lend support to the possibility of imitation through associative learning. Hoppitt and Laland (2002) used neural network modelling to show that associative mechanisms of the type proposed by ASL could be used to imitate both perceptually transparent and perceptually opaque actions. Furthermore, associative links could be formed between perceptual and motor representations even when large amounts of behavioural “noise” were introduced into the model’s learning environment. The behavioural noise is said to mimic situations where an action is performed while a non-matching action is perceived. Another study which suggests that imitation based on associative learning is possible in principle is that of Alissandrakis et al (2002). This study showed that imitation of actions between dissimilarly embodied software agents was possible using a system based on the ASL architecture.

Thus, a small number of experiments suggest that experience may play a role in the emergence of imitative ability, but the evidence is very limited. The studies of Alissandrakis et al (2002) and Hoppitt and Laland (2002) both report non-human data, while the study of Howard et al (2001) did not involve an imitation task, only action observation.

The experiments reported in Chapter 4 investigated the effect of counter-imitative training on the priming of a compatible response during action observation.
Experiment 7 demonstrated action priming by movement observation. Experiment 8 investigated how experience of performing an opposite movement to that observed (counter-imitative training), affected subsequent movement priming by action observation. If imitation is the result of an innate module, one would expect such training to have little impact on action priming. Conversely, if imitation is a result of experience, counter-imitative training should negate, or even reverse, the priming of a corresponding response.

1.5 Summary

Three theories of imitation have been outlined: the Associative Sequence Learning model (Heyes & Ray, 2000), Ideomotor Theory (e.g. Prinz 2002, 1997), and the Active Intermodal Mapping model (Meltzoff and Moore e.g. 1977, 1997). Evidence demonstrating the interaction between the perception and production of action, and observational learning of motor skills is consistent with all three theories. The theories make differential predictions regarding the possibility of 1) effector-dependent, and 2) implicit learning by action observation, and 3) the role of experience in the development of the capacity to imitate. These three issues are addressed by the experiments reported in Chapters 2, 3 and 4 respectively.
Chapter 2: Effector-Dependent Learning by Observation

Effector-dependent learning is said to have occurred when motor information learned by use or observation of one effector cannot be expressed by another. For example, knowledge required to produce a signature would be effector-dependent if an individual could sign their name with one hand, but not the other. Practice-based effector-dependent learning has been demonstrated in both monkeys (Rand, Hikosaka, Miyachi, Lu, & Miyashita, 1998) and humans (Bapi, Doya, & Harner, 2000; Marcovitch & Flanagan, in press).

Whether effector-dependent learning can occur by observation is an issue upon which the three theories of imitation can be differentiated. Both AIM and Ideomotor theories of imitation suggest that this type of learning should not be possible, while the ASL theory predicts that, under some circumstances, effector-dependent learning can occur by observation. The AIM model suggests that perceptual representations of movements are transformed into flexible, 'amodal' representations which can be translated into several different motor representations, enabling the perceived action to be performed in a variety of ways using a range of effectors. Ideomotor theory also suggests that perceived actions can lead to a variety of motor representations becoming activated. Each perceptual representation activates a number of action representations based on many levels of similarity between the perceived action and the stored action representation. Higher-order, cognitive, matching of movement goals leads to flexibility in what is matched, and the effector used to perform the matching movement.
Thus, both theories postulate that information derived from model observation is always subject to flexible, higher-order encoding, and therefore would not predict the kind of constraint on expression of that knowledge represented by effector-dependence. In contrast, ASL theory suggests that visual information from the model can activate motor representations directly, without intermediate symbolic or other higher-order representation. These observation-activated motor representations will be effector-dependent to the extent that prior visual experience of each movement component has been paired with activation of a distinct and constant muscle set. Thus, ASL theory predicts that, under conditions in which practice-based learning is effector-dependent, observational learning will also be effector-dependent.

Until recently, the idea that task observation, rather than practice, could engage effector-dependent processes of motor learning was so implausible that observation was often used as a control for this kind of learning (Stadler, 1989; Willingham, 1999). However, recent research on the human 'mirror system' (Buccino et al., 2001; Rizzolatti, Fogassi, & Gallese, 2001) and, more specifically, electrophysiological evidence of motor facilitation during action observation, has made the idea of effector-dependent learning by observation more plausible (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000). In these studies, participants observed body movements while MEPs invoked by TMS were recorded from a range of effector muscles. MEPs recorded from muscles involved in production of the observed movement were greater during movement observation than rest. For example, during thumb movement observation, MEP size was greater for the abductor pollicis brevis (APB), which is involved in executing thumb movements, than for the first dorsal
interosseus (FDI), which is active during finger movements, and this relationship between APB and FDI activation was reversed when participants observed finger movements (Maeda et al., 2002).

These electrophysiological data suggest that movement observation can activate effector-dependent motor representations stored in the primary motor cortex (Aziz-Zadeh et al., 2002). As this is likely to be necessary for effector-dependent learning by observation, these data are consistent with the hypothesis that such learning occurs. However, learning does not only involve activation of existing motor representations: formation of new connections between existing motor representations is also necessary. Therefore these electrophysiological data are insufficient in determining whether new sequences can be learned in an effector-dependent fashion by observation.

To investigate effector-dependence of observational learning, the present study used an SRT task. In a typical version of this task, a stimulus appears in one of several locations on each trial, and the participant presses a key corresponding to that location. The stimulus follows a predictable repeating sequence and, after many cycles, participants provide evidence of sequence knowledge by responding more slowly when the sequence is changed than when stimuli were presented in the training sequence. The SRT task is an ideal tool to study effector-dependence of observation learning for several reasons. First, it can be readily adapted to investigate observational learning by requiring participants to watch a model performing the task during the training phase, before completing tests in which they press the keys themselves. Second, SRT tasks assess sequence learning, the kind of learning that
distinguishes activation of pre-existing motor representations from acquisition of 'new' motor representations. Finally, there is evidence that motor learning is involved when participants perform the task themselves (Mayr, 1996; Willingham, 1999; Willingham, Nissen, & Bullemer, 1989). For example, Willingham (1999, Experiment 3) added to the SRT task a transfer test in which the stimulus-response mapping was changed so that, relative to training, one group of participants pressed the same sequence of keys but saw new stimuli, whereas another group pressed a different sequence of keys but saw the same stimuli. Transfer to the new mapping occurred only if the motor sequence was kept constant.

Kelly and Burton (2001) failed to find evidence of observational learning of any kind (perceptual or motoric) when they compared the SRT performance of practice participants with that of observers who watched a practice participant during training on a 12-item ambiguous sequence. However, Heyes and Foster (2002) reported evidence of observational learning when they compared participants who had observed an expert responding to a six-item unique sequence with controls who had performed an unrelated anagram task during training. Therefore, in the present study, to ensure that observational learning would be detected, the same six-item sequence and kind of comparison group was used as in Heyes & Foster (2002).

Many studies have reported implicit learning of 10- or 12-item ambiguous sequences in the SRT task, i.e. sequence knowledge that is not accessible to conscious awareness (e.g. Seger, 1997; Willingham, 1999). A six-item unique sequence, of the kind used in the present study, is very simple compared with the sequences used in this previous work, and therefore is unlikely to be learned implicitly. However, it would be
interesting if observational learning of a six-item unique sequence could be shown to be both effector-dependent and explicit, because such evidence would be incompatible with a recent model of motor skill learning (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). This model proposes that effector-dependent learning is typically implicit, whereas effector-independent learning is typically explicit. Therefore, in addition to asking whether participants' knowledge was effector-dependent, it was investigated whether knowledge was implicit or explicit using free generation (Experiment 1) and recognition (Experiment 2) tests (Shanks & Johnstone, 1999).

In a standard SRT task, practice-based learning is demonstrated by comparing RTs to stimuli presented in the training sequence and in an alternative sequence. However, in the present study observers are compared with controls who were not exposed to a sequence during training. In this case observational learning is indicated when the increase in RT upon transfer to the new sequence is greater for observers than controls. Thus, the control group provides a baseline, and if the introduction of a new sequence delays responding more in the observers than in the controls, there is evidence that the former group learned the sequence by observation. This logic applies to both of the control groups used in the present study. In Experiment 1, control participants were untrained (Dienes & Altmann, 2003; Perruchet & Reber, 2003), they performed an unrelated anagram task during the training phase, and in Experiments 2 and 3 controls observed a model performing the SRT task when order of target presentation was randomly determined.

To find out whether observational learning had been effector-dependent, participants in all experiments were given two transfer tests following the initial test of sequence
knowledge. In Experiments 1 and 2, each transfer test consisted of a block of trials in which stimulus presentation was determined by the training sequence, followed by a block in which it was determined by the new sequence. In one of these tests, the 'stimulus transfer test', the stimuli appeared in a vertical rather than a horizontal array of boxes on the screen, and responses were made, as during training, with the fingers. In the other, 'response transfer test', the stimuli appeared in a horizontal array, as they had during training, but participants were required to respond using their thumbs rather than their fingers. If RT increase upon transfer to the new sequence is greater for observers than controls on the stimulus transfer test only, then effector-dependent learning will be suggested. Observers would be able to use their sequence knowledge when the stimuli were presented in a different spatial array, but not when responding with different effectors (Stadler, 1989).

2.1 Experiment 1

The first experiment involved two groups of participants, which received different treatment in the training phase: Group Observe Sequence watched the experimenter's fingers as he performed the SRT task, whereas Group Control completed an unrelated anagram task. After initial testing for sequence knowledge, they were given transfer tests in which all participants responded to the training sequence and then to a new sequence under two conditions: when the stimulus array was unchanged but they were required to use their thumbs rather than their fingers to respond (response transfer test), and when responses were made with the fingers, but the stimuli appeared in a vertical rather than a horizontal array (stimulus transfer test).
If, in both transfer tests, transition to the new sequence is associated with a greater increase in RT in Group Observe Sequence than in Group Control, it would imply that sequence knowledge learned by observation can withstand alterations of both stimulus array and response effector. This would suggest that the observers' sequence knowledge is encoded in an effector-independent, symbolic fashion (e.g. linguistically or numerically). Alternatively, if observers' performance does not differ from that of controls when both groups respond to a vertical rather than a horizontal stimulus array, but does when responses are made with the thumbs, learning of stimulus locations is implied. This is unlikely given that the observers in Experiment 1 could not see the stimuli on the screen during training. Effector-dependent learning of a finger movement sequence by observation would be implicated if the performance of observers and controls was only different on the stimulus transfer test. In this case transition to the new sequence would cause greater RT elevation in observers than in controls when responses are made to a vertical rather than a horizontal stimulus array, but not when responses are made with thumbs rather than fingers. This outcome would implicate effector-dependent learning by observation by showing that, relative to that of controls, the observers' sequence knowledge transfers across alterations in the stimulus array, but not to a situation where different effectors are used to perform the task.

2.1.1 Method

Participants. Twenty-four students at University College London (UCL) participated in the experiment, 12 in each of Groups Observe Sequence and Control. Their mean age was 23.6 years, eight were male, and each was paid a small honorarium for their
participation. As is usual in SRT experiments (see e.g. Curran & Keele, 1993; Seger, 1997), participants (n=5) who made more than 10% errors during the random and initial test blocks were replaced.

Stimuli & Apparatus. Stimulus presentation, RT measurement, and response recording were all implemented on IBM-compatible PCs with 43 cm colour monitors and standard QWERTY keyboards. Six boxes were presented in a horizontal row in the centre of the screen, drawn with black lines against a grey background. The boxes were 2.2 cm wide and 1.2 cm high, spaced 1-cm apart, and viewed at a distance of approximately 60 cm. A white asterisk (Arial font size 36, subtending approximately 0.5° of visual angle) appeared in the centre of one of these boxes on each target location trial. Target locations are referred to as 1-6 from left to right. Participants were instructed to indicate locations 1 - 6 as quickly as possible by using the X, C, V, B, N, and M keys located across the bottom of the keyboard, respectively. They operated the X, C, and V keys with the ring, middle, and index fingers of their left hand, and the B, N, and M keys with the index, middle and ring fingers of their right hand, respectively.

Each block consisted of 100 target location trials. Incorrect responses were signalled by a tone. A trial ended when a participant pressed the correct key, at which time the target was erased. The next trial began 200 ms later. RT was measured from target onset until a correct response had been made.

Procedure. Participants were told that they were taking part in a choice RT task designed to measure their speed of response. For all participants, the experiment had 5
phases: 1) familiarization, 2) training, 3) initial testing, 4) transfer, and 5) free generation. The two groups received identical treatment in all phases except the training phase. During training, Group Observe Sequence watched the experimenter's fingers as he performed the SRT task, and Group Control completed anagram problems for a comparable period of time.

Familiarization. In the familiarization phase, participants were given one block of target location trials in which the order of target presentation was randomly determined.

Training. Group Observe Sequence were instructed to watch the experimenter's fingers as he completed six blocks of target location trials, in which the sequence of targets was 2-5-1-4-6-3. Each block of 100 trials included 16 repetitions of the whole training sequence, and began at a random point in that sequence. Observers were seated to the right, and just behind the experimenter, on a chair which had been raised to give them a slightly elevated view of his fingers on the keyboard. The screen was turned away from the observers so that they could not see the target stimuli to which the experimenter was responding. Before the first training block participants were told, “Please pay close attention to the experimenter’s hands as he completes the task. It has been shown that the more closely you attend to the hands, the better you will do in the later stages of the experiment”. The experimenter provided a model of expert performance, with a mean RT ranging from 273 ms (SE = 7) to 299 ms (SE = 9) across the 6 blocks. Error rate varied from 0 to 2 %. For the duration of the training period (8 minutes), participants in Group Control solved anagram problems.
Initial testing. The initial test of sequence learning consisted of three blocks of target location trials, completed by all participants. In the first and last of these blocks, targets were presented in the training sequence, i.e. 2-5-1-4-6-3. In the second block, they were presented in a new, six-item unique sequence: 4-2-6-3-1-5.

Transfer. The order of the stimulus transfer and the response transfer tests was counterbalanced, with half of the participants in each group completing the stimulus transfer test first. Each transfer test consisted of two blocks of trials. In the first, targets were presented in the training sequence, and in the second they were presented in the new sequence. In the stimulus transfer test, the stimulus boxes were arranged in a vertical, rather than a horizontal, line in the centre of the computer screen. As during training, participants were required to respond to targets 1-6 (now running from the top to the bottom of the screen) using the ring, middle and index fingers of each hand, applied to keys X, C, V, B, N and M. In the response transfer test, the stimulus boxes were arranged in a horizontal line as they were during training, but participants were required to respond with their thumbs rather than their fingers. The left thumb was used to operate the X, C and V keys, and the right thumb was used to operate the B, N and M keys.

Free generation. Participants were informed for the first time that the asterisks had followed a repeating sequence during the experiment. They were asked to press the keys 100 times, attempting to generate the sequence that they had experienced during training and at the beginning of each subsequent test. They were told that they could proceed at their own pace, and that their keypresses would have no effect on the
stimulus array, i.e. a static image of the horizontal line of boxes representing stimulus locations.

2.1.2 Results and Discussion

A mean RT for each participant in each block was calculated after exclusion of RTs greater than 1000ms (as is usual in SRT experiments, see e.g. Reber & Squire, 1998). Each analysis of RT data was accompanied by a parallel analysis of error data. The error data from all three experiments are shown in Table 1. The results of error analyses are reported only if they yielded significant effects or interactions. For all analyses, all significant effects are reported.

<table>
<thead>
<tr>
<th>TEST</th>
<th>Initial Test</th>
<th>Stimulus Transfer Test (Expts 1 and 2)</th>
<th>Anatomical Transfer Test (Expt 3)</th>
<th>Response Transfer Test (Expts 1 and 2)</th>
<th>Response Location Test (Expt 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Training</td>
<td>New</td>
<td>Training</td>
<td>New</td>
<td>Training</td>
</tr>
<tr>
<td><strong>SEQUENCE</strong></td>
<td><strong>TRAINING</strong></td>
<td><strong>NEW</strong></td>
<td><strong>TRAINING</strong></td>
<td><strong>NEW</strong></td>
<td><strong>TRAINING</strong></td>
</tr>
<tr>
<td>Observe Sequence</td>
<td>2.8/0.4</td>
<td>3.0/0.7</td>
<td>4.4/0.8</td>
<td>6.6/0.8</td>
<td>5.2/1.4</td>
</tr>
<tr>
<td>Control</td>
<td>3.0/0.7</td>
<td>3.9/0.8</td>
<td>4.2/0.9</td>
<td>5.5/0.9</td>
<td>6.5/1.6</td>
</tr>
<tr>
<td>Observe Sequence</td>
<td>1.9/0.6</td>
<td>3.2/0.6</td>
<td>7.3/1.5</td>
<td>7.2/2.3</td>
<td>4.6/1.2</td>
</tr>
<tr>
<td>Control</td>
<td>2.3/0.5</td>
<td>2.4/0.7</td>
<td>4.7/0.8</td>
<td>5.3/1.0</td>
<td>7.9/1.8</td>
</tr>
<tr>
<td>Observe Sequence</td>
<td>3.9/0.5</td>
<td>5.1/0.8</td>
<td>17.4/1.4</td>
<td>16.0/1.8</td>
<td>14.9/1.4</td>
</tr>
<tr>
<td>Control</td>
<td>2.6/0.4</td>
<td>2.7/0.5</td>
<td>12.3/2.4</td>
<td>11.8/2.1</td>
<td>9.6/1.5</td>
</tr>
</tbody>
</table>

Table 1. Mean (+- standard error) percentage error for training and new sequences in initial and transfer tests for each group in Experiments 1-3.
One-way ANOVA with group as a between-subjects factor indicated that in the familiarization phase, when participants were responding to random targets, the RTs of observers (M = 597, SEM = 14) and controls (M = 598, SEM = 22) did not differ (F<1).

Figure 1 presents mean RTs to training and new sequence blocks during initial and transfer testing for each of the two groups of participants. In the initial test, RTs in the first and third blocks, when participants were responding to the training sequence, were compared with RTs in the second block, when they were responding to a new sequence. In order to analyse these data a difference score was calculated for each participant by subtracting their average RT on the sequence with which they were trained, from their RT on the new sequence block. These difference scores were then analysed using univariate ANOVA with group (Observe Sequence and Control) as the between-subjects factor. A significant effect of group was revealed (F(1, 22) = 5.88, p = 0.02). Thus, introduction of the new sequence was associated with a greater increase in RTs in the observers than the controls, suggesting that the former group had learned the sequence by observing the experimenter's fingers while he was performing the task.
Observe Sequence

Figure 1 - Mean RT in initial and transfer test blocks for groups that had observed a model's fingers as he responded to the training sequence (Observe Sequence) or solved unrelated anagram problems (Control) during training in Experiment 1.

RT data from the stimulus transfer test were analyzed using two-way ANOVA with group (Observe Sequence and Control) and test order (before and after the response transfer test) as between-subjects factors. This revealed a significant effect of group ($F_{(1,20)} = 6.15, p = 0.02$). When the same two-way ANOVA was applied to RT data from the response transfer test, the effect of group was not reliable ($F<1$). There were no effects of test order in any analysis.

Thus, when the stimulus array, which was horizontal during training and initial testing, was presented vertically, introduction of the new sequence had a more detrimental effect on the performance of observers than on that of controls. This indicates that, in spite of the change in the stimulus array, the observers were still able to use their sequence knowledge. However, when participants were required to use
their thumbs rather than their fingers to press the response keys, the transition from the training to the new sequence had the same impact on the performance of observers and controls. This implies that, when responding with their thumbs, the observers were unable to use the sequence knowledge they had gained during training, and is therefore consistent with the hypothesis that the sequence knowledge they acquired by observation was effector-dependent.

In the free generation test, participants created sequences of 100 key presses based on what they had learned about the training sequence. Data were coded as 98 consecutive response triplets and the number of triplets that were consistent with the training sequence (2-5-1-4-6-3), was compared with the number that were consistent with the new sequence (4-2-6-3-1-5). A difference score was calculated as in the analysis of RT data, the number of triplets produced from the new sequence was subtracted from the number of triplets produced from the training sequence. Thus, if a participant generated the sequence 2-5-1-5-4 at some point during the free generation test, this would be coded as triplets 2-5-1, 5-1-5, and 1-5-4. The first of these triplets is consistent with the training sequence, whereas the third is consistent with the new sequence. Given that the participants had already completed three blocks of trials with the 'new' sequence, this was a conservative test of explicit knowledge, but it was passed by the observers. Figure 2 shows the mean number of training and new triplets generated by participants in the two groups. Univariate ANOVA with group (Observe Sequence and Control) as a between-subjects factor, indicated a significant effect of group ($F_{(1,22)} = 7.00, p = 0.02$)
Figure 2 Mean (+- standard error) number of training and new triplets generated in the free generation test by groups that had observed a model's fingers as he responded to the training sequence (Observe Sequence) or solved unrelated anagram problems (Control) during training in Experiment 1.

The results of Experiment 1 suggest that participants can learn a six-item sequence by observing a model's responses to the SRT task, and that the sequence knowledge gained through observation was effector-dependent; it could only be expressed by the effectors observed during training. Observers were also aware of their knowledge and were able to freely generate more of the sequence than controls.

2.2 Experiment 2

Experiment 1 provided evidence of effector-dependent, explicit, sequence learning by observation using an untrained control group. While the observers were watching the experimenter perform the SRT task, control participants in Experiment 1 completed anagram problems. This kind of control is of limited value because it means that, in
addition to being unable to acquire sequence information by observation, controls have less opportunity than observers to familiarize themselves with general task demands. As a consequence of being less familiar with, for example, response locations, untrained control participants may acquire sequence information more slowly than observers during test blocks in which all participants respond to the training sequence. If this is the case, observers may provide evidence of more sequence knowledge in initial and transfer tests, not because they acquired this information by observation, but because they learned more than controls on test. To overcome this problem, a more subtle control procedure was used in Experiment 2. During the training phase, both groups watched a model's fingers. As in Experiment 1, the model observed by Group Observe Sequence was responding to stimuli presented in the training sequence. However, the model observed by control participants, Group Observe Random, was responding to stimuli presented in random order.

Experiment 2 differed from Experiment 1 in two further respects. First, to achieve better stimulus control, the model's finger movements were presented on video, rather than live. Second, a recognition test, rather than a free generation test, was used at the end of the experiment to assess whether sequence knowledge was implicit or explicit. This substitution was made because, as a measure of explicit knowledge, the free generation test may be contaminated by sensitivity to implicit motor learning. The observers in Experiment 1 may have passed the free generation test, not because their knowledge of the sequence was consciously accessible, but because they executed a learned motor program, the contents of which were not available to conscious awareness. Motor learning of this kind could not explain success on a recognition test
in which participants respond to, and then rate their familiarity with, sequences derived from the training sequence and from an alternative, new sequence.

If participants are able to learn effector-dependent, explicit, sequence information by observation, the pattern of results obtained in Experiment 2 should be the same as that obtained in Experiment 1.

2.2.1 Method

Participants. A further 24 volunteers participated in the experiment, 12 in each of Groups Observe Sequence and Observe Random. Their mean age was 30.08 years and 12 were male. Two participants who made more than 10% errors during the random and initial test blocks were replaced.

Procedure. The procedure was exactly the same as for Experiment 1 except as noted. During the training phase, the control participants, in Group Observe Random, observed a model's fingers as he responded to target stimuli presented in random order. Participants in both groups, Observe Screen and Observe Random, viewed video recordings of the model's finger movements played full screen on a 38-cm, TFT Active Matrix Display computer screen. Each of the model's hands subtended approximately 26.5° of visual angle. The images were recorded using a Sony digital camcorder, encoded as AVI (720 x 576 pixels) files, and displayed on an IBM compatible laptop computer using Microsoft Windows Media Player. The video frame included all eight of the model's fingers, the response keys, and four rows of keys above the response keys. The viewing angle was similar to that of ones own
hands while typing (see Figure 3). When filmed for Group Observe Sequence, the model's mean RT ranged from 347ms to 398 ms across blocks, and he made no errors. When filmed for Group Observe Random, his mean RT ranged from 501 ms to 543 ms across blocks, and he made no errors.

![Figure 3 A frame from the training video presented to the Observe Sequence group in Experiments 2 and 3, showing the model making a response with the index finger of his left hand.](image)

In the final phase of the experiment, participants were given a recognition test. They were told that they would be presented with sequences of six asterisk locations, presented in the standard, horizontal array of boxes. They were to respond to these stimuli as they had during training and initial testing, and then give a rating of how confident they were that the test sequence was the same as the sequence used during training and initial testing. Ratings were made on a scale from 1 to 6, where 1 = certain I have not seen the sequence before, 2 - fairly certain I have not seen the sequence before, 3 - guess I have not seen the sequence before, 4 - guess I have seen the sequence before, 5 - fairly certain I have seen the sequence before, and 6 - certain
I have seen this sequence before. Both ratings and trial-by-trial RTs were recorded.

There were 12 test sequences in total, presented in random order. Six 'old' sequences were derived from the training sequence, and six 'new' sequences were derived from the sequence: 1-3-5-4-2-6. One sequence in each of these groups started at each serial location.

2.2.2 Results and Discussion

Results were analyzed in the same way as those of Experiment 1. One-way ANOVA indicated that in the familiarization phase, when participants were responding to random targets, the RTs of Group Observe Sequence (M = 611, SEM = 20) and of Group Observe Random (M = 610, SEM = 22) did not differ (F<1).

Figure 4 presents mean RTs to training and new sequences during initial and transfer testing for each of the two groups. Univariate ANOVA of the initial test data indicated a significant effect of group ($F(1, 22) = 5.92, p = 0.02$). Thus, introduction of the new sequence was associated with a greater increase in RTs in the Group Observe Sequence, than in Group Observe Random, indicating observational learning of the sequence by participants in the former group.
Figure 4 Mean RT in initial and transfer test blocks for groups that had observed a model's fingers as he responded to the training sequence (Observe Sequence) or to a random sequence (Observe Random) during training in Experiment 2.

As in Experiment 1, two-way ANOVA of the RT data from the stimulus transfer test yielded a significant effect of group ($F_{(1,20)} = 4.13, p = 0.05$), but the same analysis of the response transfer test indicated no significant effects or interactions.

Analysis of the recognition test followed a different format from that of the test blocks. The purpose of the recognition test was to assess how aware members of each group were of any sequence knowledge they have acquired. To this end, two sources of data were collected during the test; mean RT to each sequence and a rating of its familiarity. Evidence of implicit knowledge was provided when members of a group demonstrated sequence knowledge by responding faster to training than new sequence fragments, while rating both sequences as equally familiar. In contrast, explicit knowledge was shown when training sequences were responded to faster than new sequences, and were rated as more familiar. Separate analyses were performed on the
RT and rating data to identify sequence knowledge shown by any group on each measure. For each participant, average RT to, and average rating of, training and new sequences was calculated. Group means are given in Table 2.

<table>
<thead>
<tr>
<th>Group</th>
<th>Mean Rating Training (SEM)</th>
<th>Mean Rating New (SEM)</th>
<th>Mean RT Training (SEM)</th>
<th>Mean RT New (SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observe Sequence</td>
<td>4.13 (0.24)</td>
<td>3.26 (0.16)</td>
<td>538 (26.9)</td>
<td>592 (22.2)</td>
</tr>
<tr>
<td>Observe Random</td>
<td>3.79 (0.16)</td>
<td>3.86 (0.13)</td>
<td>563 (28.8)</td>
<td>575 (26.9)</td>
</tr>
</tbody>
</table>

Table 2. Mean (+- standard error) reaction times (RTs) and recognition ratings given to training and new sequences by groups that had observed a model's fingers as he responded to the training sequence (Observe Sequence) or to a random sequence (Observe Random) during training in Experiment 2.

Two-way ANOVA applied to the RT data, with group (Observe Sequence and Observe Random) and sequence type (training and new) as factors, indicated significant effects of sequence type, $F_{(1, 22)} = 9.61, p = .005$, and a marginally significant group x sequence interaction, $F_{(1,22)} = 4.00, p = .06$. Simple effects analysis revealed a significant difference in RT to training and new sequences for the Observe Sequence group ($F_{(1, 22)} = 13, p = 0.002$), but not for the Control group ($F<1$).

Parallel analysis of the recognition rating data yielded the same pattern of results; a main effect of sequence type, $F_{(1,22)} = 4.19, p = .05$, and a significant interaction, $F_{(1,22)} = 5.80, p = .03$. Simple effects analysis showed that the difference in ratings given to training and new sequences was significant for the Observe Sequence group ($F_{(1, 22)} = 9.92, p = 0.005$), but not for the Control group ($F<1$).
Thus, although Experiment 2 involved a more subtle control group, video presentation of finger movement stimuli, and a recognition test of explicit knowledge, the pattern of results was exactly the same as that of Experiment 1.

2.3 Experiment 3

In combination, Experiments 1 and 2 provide compelling evidence that participants can learn a six-item sequence by observing a model's finger movements, and that this sequence knowledge is accessible to conscious awareness. It could be argued, however, that the foregoing experiments do not provide equally strong evidence that observational sequence learning can be effector-dependent. This hypothesis rests on the finding that, in Experiments 1 and 2, the transition from the training sequence to a new sequence was associated with greater RT elevation in observers than in controls when they were responding to targets in a transformed stimulus array, but not when they were responding with their thumbs rather than their fingers. This finding is consistent with effector-dependence of observational sequence learning, but is also susceptible to an alternative explanation. It is possible that what was learned by observation was a sequence of response locations encoded in an effector-independent fashion, either symbolically or as locations in egocentric space (Willingham, 1999). If the stimulus transfer test, in which the stimulus array was vertical, and the response transfer test, in which participants responded with their thumbs, were of equal sensitivity, effector-independent knowledge of a sequence of response locations should be evident in both. However, it could be that, in Experiments 1 and 2, no evidence of sequence knowledge was detected in the response transfer test because that test was less sensitive than the stimulus transfer test. The participants may have
found it difficult to use their thumbs to press the keys, and this may have interfered with expression of effector-independent sequence knowledge about response locations.

To address this problem, an alternative transfer test procedure was used in Experiment 3. After training and initial testing, all participants crossed their hands on the keyboard for two transfer tests. This manipulation allowed the sequence of finger movements to be dissociated from the sequence of response locations. The sequence of finger movements made during training produced a novel sequence of response locations and vice versa. The anatomical transfer test compared RTs to a sequence of screen targets which preserved the finger movement sequence used during training with RTs to a sequence of screen targets which produced a new sequence of finger movements. The response location transfer test compared RTs to the training sequence of screen targets with RTs to a new sequence of screen targets. The training sequence of screen targets in the response location test preserved the sequence of response locations used during training, but neither of the target sequences in the anatomical test preserved the training sequence of response locations. Therefore, if Group Observe Sequence learned a sequence of response locations during training, but not an effector-dependent sequence of finger movements, then, relative to Group Observe Random, they should be slower to respond to the new than to the training sequence in the response location test but not in the anatomical test. In contrast, if Group Observe Sequence learned an effector-dependent sequence of finger movements during training and did not learn a sequence of response locations, then, relative to Group Observe Random, they should be slower to respond to the new than to the training sequence in the anatomical test but not in the response location test.
The occurrence of a group by sequence interaction effect in both tests would imply that Group Observe Sequence had learned both an effector-dependent sequence of finger movements and a sequence of response locations during training.

2.3.1 Method

Participants. A further 48 volunteers participated in the experiment, 24 in each of Groups Observe Sequence and Observe Random. Their mean age was 22.17 years and 15 were male. Eight participants who made more than 10% errors during the random and initial test blocks were replaced.

Procedure. The procedure was exactly the same as for Experiment 2 except as noted. The experiment had four phases: familiarization, training, initial testing and transfer.

Transfer. After initial testing, all participants were asked to cross their hands so that keys X, C and V were operated by the index, middle and ring finger of the right hand, respectively, whereas keys B, N, and M were operated by the ring, middle and index fingers of the left hand, respectively. With their hands crossed, they completed, in counterbalanced order, two transfer tests each consisting of three blocks of 100 target location trials.

In the first and third 'training' blocks of the anatomical test, screen targets were presented in the sequence 5-2-4-1-3-6. This sequence has no transitions in common with the training sequence of screen stimuli (2-5-1-4-6-3), i.e. each target is immediately followed by a different target than it was during training. Given that the
target locations and the response locations were spatially compatible, this also means that the sequence of response locations associated with this sequence had no transitions in common with the training sequence of response locations. However, in the context of the anatomical test, the target sequence 5-2-4-1-3-6 constitutes the training sequence because correct responses occur in the finger movement sequence observed during training. Where R = right, L = left, i = index, m = middle and r = ring, this sequence was Lm-Rm-Lr-Ri-Rr-Li. In the second 'new' block of the anatomical test, screen targets were presented in the sequence 2-1-5-3-6-4. This sequence has no transitions in common with the training sequence of targets and response locations, and just one transition (Rr-Li) in common with the training sequence of finger movements.

In the first and third blocks of the response location transfer test, target stimuli were presented in the training sequence, i.e. the sequence of screen stimuli and response locations had all six transitions in common with those used during training. In the second block, targets were presented in the sequence 4-2-6-3-1-5, which has only one transition in common with the training sequence. Given that the hands were crossed, both of the sequences presented in the response location transfer test produced finger movement sequences which did not have any transitions in common with the finger movement sequence used during training.

2.3.2 Results and Discussion

Owing to the difficulty of performing the task with crossed hands, RTs greater than 1000ms were not removed from the data prior to analysis. One-way ANOVA
indicated that in the familiarization phase, when participants were responding to random targets, the RTs of Group Observe Sequence (M = 526, SEM = 12) and of Group Observe Random (M = 552, SEM = 13) did not differ (F(1, 46) = 2.04).

Figure 5 presents mean RTs to the training sequence and the new sequence during initial and transfer testing for each of the two groups. Univariate ANOVA of the initial test data indicated a significant effect of group (F(1, 46) = 6.78, p = 0.01). Thus, as in the previous experiments, introduction of the new sequence was associated with a greater increase in RTs in the Group Observe Sequence, than in Group Observe Random, indicating observational learning of the sequence by participants in the former group.

Figure 5 Mean RT in initial and transfer test blocks for groups that had observed a model's fingers as he responded to the training sequence (Observe Sequence) or to a random sequence (Observe Random) during training in Experiment 3.
The anatomical and response location tests were each analyzed in the same way as initial test data. Two-way ANOVA of the RT data from the anatomical test, in which group and transfer test order were between-subjects factors, yielded a significant effect of group ($F_{(1,44)} = 5.10, p = 0.03$). This effect of group shows that the difference in RT between training and new sequence blocks was greater for Group Observe Sequence than Group Observe Random, and implies that Group Observe Sequence had learned an effector-dependent sequence of finger movements by observation.

The results of the response location test did not provide any evidence of effector-independent learning by observation of a sequence of response locations. Two-way ANOVA of the RT data from this test indicated that the effect of group was not significant ($F<1$).

Inspection of mean RT to training and new sequences suggests that both groups had some knowledge of the training sequence of response locations by the time they completed the response location test. However, the impact on RTs of the transition from the training to the new sequence was the same for the two groups, and therefore the response location test provided no evidence that participants in Group Observe Sequence acquired knowledge about the sequence of response locations by observation, rather than during testing.

In combination, the results of the anatomical and response location tests are consistent with the hypothesis that Group Observe Sequence learned by observation an effector-dependent sequence of finger movements, and not a sequence of response locations.
The critical question addressed by the present experiments is whether observational learning of a finger movement sequence can be effector-dependent. Experiments 1 and 2 provided evidence of effector-dependence in the form of a dissociation between two transfer tests: Relative to controls who had not been exposed to the sequence during the training phase, participants who had observed the model performing the finger movement sequence responded faster to the training sequence than to a novel sequence when they were using their fingers to press the keys (stimulus transfer test), but not when they were using their thumbs (response transfer test). Experiment 3 provided further evidence of effector-dependence by controlling for the possibility that the dissociation reported in Experiments 1 and 2 was due to a difference between the stimulus and response transfer tests in their sensitivity to effector-independent knowledge of a sequence of response locations. For both transfer tests in Experiment 3, participants' hands were crossed on the keyboard. In the anatomical crossed-hands test, stimuli were presented in two sequences, both of which generated a sequence of response locations distinct from that observed during training. In spite of this, relative to controls, participants who had observed the model performing the finger movement sequence during training responded faster to stimuli that generated the observed finger movement sequence than to stimuli that generated a different finger movement sequence. Thus, the skill learned by observation did not transfer across fingers. The two stimulus sequences presented in the response location crossed-hands transfer test both generated sequences of finger movements that differed from those seen by the experimental group during training, but one of them did, and the other did not, conserve the training sequence of response locations. Participants who had observed
the model performing the finger movement sequence responded faster to the stimulus sequence which generated the training sequence of response locations than to the alternative stimulus sequence, but this effect was also found in the control group. This implies that, in addition to their effector-dependent knowledge of the sequence of finger movements, the experimental group had some knowledge of the sequence of response locations. However, it also suggests the information about response locations was acquired during testing, i.e. while practicing, rather than by observation.

Effector-dependent learning by observation of a finger movement sequence is consistent with the ASL model of observational learning because it proposes that movement observation can activate motor representations directly, i.e. without intermediate representation in a code that is neither perceptual nor motoric. The results of the present experiments are harder to reconcile with theories which assume that observational learning is invariably mediated by amodal representations (AIM). These results are also hard to reconcile with the view of imitation described by Ideomotor Theory, in which imitation always has the potential to be carried out by higher-order, effector-independent, cognitive action representations. Neither AIM nor Ideomotor theories of imitation specify the nature of amodal or higher-order, cognitive codes, but they both imply that these codes are of a kind that supports a broad range of inferences. Therefore, to accommodate the transfer effects found in the present experiments, these theories would have 1) to assume that participants initially represented the observed sequence of finger movements in a symbolic or amodal code with anatomical content (e.g. in linguistic form: "left middle - right middle - left ring - right index - right ring - left index") rather than abstract content (e.g. "response location 2 - 5 - 1 - 4 -6 -3), and 2) to explain why, given background knowledge of
finger locations and corresponding screen locations, the former could not be translated into the latter so that sequence knowledge could be used in response transfer (Experiments 1 and 2) and response location transfer (Experiment 3) tests.

In connection with the first of these requirements, it is important to note that the results of the free generation and recognition tests do not show that the participants in the experimental groups had sequence knowledge represented in a symbolic or amodal code with anatomical content. As discussed in the introduction to Experiment 2, successful performance in the free generation test may reflect implicit, or consciously inaccessible, effector-dependent learning. The recognition test provides a better measure of explicit knowledge, but successful performance in this kind of test may be based on a consciously accessible experience of perceptual-motor fluency (Shanks & Johnstone, 1999). Thus, when participants respond to a sequence and then immediately rate its familiarity, it does not imply that their rating is based on consciously accessible knowledge that, for example, "movement of the left middle finger is followed by movement of the right middle finger". Instead, participants may base their rating on conscious perception of the fluency with which they responded to the sequence, and movement fluency may itself be a function of nonsymbolic, effector-dependent sequence representation.

These results imply that observational sequence learning can be both explicit and effector-dependent. This is consistent with previous studies of observational learning using the SRT task which report evidence that observers had acquired sequence knowledge only when post-test interview indicated that they had explicit knowledge of the sequence (Howard, Mutter, & Howard, 1992; Kelly & Burton, 2001;
Willingham, 1999). However, the present results are not consistent with a model of motor skill learning which proposes that effector-dependent knowledge is implicit, whereas effector-independent knowledge is explicit (Hikosaka et al, 2002). In combination with recently reported evidence of implicit, effector-independent, practice-based learning (Japikse, Negash, Howard, & Howard, 2003), the present results therefore imply that these relationships are not invariant either for practice-based or for observational sequence learning.

In Experiment 3, participants who had observed the model performing the finger movement sequence did not show any advantage over controls in the response location transfer test, and therefore this test did not provide any evidence of observational learning. However, both groups responded faster with the training sequence of response locations than with the alternative sequence, a finding which is consistent with Willingham's (1999) suggestion that performance (rather than observation) of an SRT task supports learning about response locations.

In conclusion: Experiments in this chapter have suggested that effector-dependent representations can be formed by observation. This conclusion is incompatible with both AIM and Ideomotor theories of imitation due to their specification of flexible, higher-order representations which enable (AIM), or accompany (Ideomotor Theory), imitation. In contrast, the formation of effector-dependent representations through observation is predicted by ASL.
Chapter 3: The Role of Awareness in Imitation

Whether imitation is invariably an active, intentional, goal-directed process is a topic of theoretical dispute. The AIM model of imitation argues that imitation always has the above qualities. According to this model, the process of imitation is conscious and effortful in nature. Initially, the goal of a model's action is inferred from the model’s movements (Meltzoff, 1995), and enables the imitator to decide which movement features to imitate. The present state of the imitator’s body is then actively compared with the desired state, and corrections are made if necessary (Gleissner, Meltzoff, & Bekkering, 2000; Meltzoff & Decety, 2003; Meltzoff & Moore, 1997). This view of imitation can be contrasted with those of the ASL and Ideomotor theories of imitation. Both theories posit that, under certain conditions, imitation may occur automatically, without effortful processing (see Chapter 1 for a more detailed discussion).

Research which has investigated the intentionality of imitation suggests that in a variety of situations imitation can occur automatically, without intention, and in some cases counter to intention. Examples of unintentional imitation include studies detailing; unconscious and involuntary mimicry of other's mannerisms and behaviour in social situations (e.g. Chartrand & Bargh, 1999; Lakin and Chartrand, 2003), and compulsive imitation after frontal lobe damage (Lhermitte, Pillon, & Serdaru, 1986). However, awareness in the former group of experiments is measured using a verbal report measure which has been argued to be insufficient to detect unconscious knowledge of behaviour (see section 1.4.2 of Chapter 1). The second group of experiments demonstrate unconscious imitation in brain-damaged patients, and the generalisability of these results to healthy adults has not been established.
Research demonstrating movement compatibility effects (see section 1.3.1.1 of Chapter 1) also suggest that imitation can occur unconsciously. These studies imply that perception of an action primes the production of that action in the perceiver even when observed movements are task-irrelevant (Brass, Bekkering, Wohlschlager, & Prinz, 2000; Stürmer, Aschersleben, & Prinz, 2000), or opposed to the required response movement (Brass, Bekkering, & Prinz, 2001; Kerzel & Bekkering, 2000).

However, even this research does not definitively show unconscious imitation: even though participants were not instructed to imitate in these experiments they may still be prompted to imitate by action observation, or be aware of the effect of the observed movement on their behaviour. In addition, these experiments do not use an imitation task: participants make either a pre-defined response to any observed movement or do not base responses on the observed movement type.

Thus, several research areas lend support to the hypothesis that imitation may occur unconsciously. However, problems or limitations of this research mean that it cannot be concluded with any degree of certainty that unconscious imitation does occur. This chapter investigates whether imitation of novel behaviour, (in particular of novel finger-movement sequences), can occur automatically. If unconscious imitation is demonstrated, then the AIM characterisation of imitation as an active, effortful, goal-directed process will be called into question. Methodological issues in experiments 2 and 3 (Chapter 2) mean that these experiments were not sufficient in establishing how aware participants were of any sequence knowledge gained through observation. The tests of awareness in these experiments were completed after transfer tests designed to
elucidate sequence encoding. Thus, the results of the tests of awareness may have been contaminated by performance of the transfer tests.

In order to investigate whether learning through imitation is conscious or unconscious, the SRT task used in Chapter 2 will again be utilised here, but without the addition of transfer tests. This task, in combination with a test of explicit knowledge, has been widely used to study participants’ awareness of learned information (e.g. Nissen & Bullemer, 1987; Shanks & Channon, 2002; Shanks & Johnstone, 1999; Willingham, Nissen, & Bullemer, 1989).

Using this task, some researchers have claimed to show practice-based learning which is not accompanied by awareness i.e. implicit knowledge. These experimenters have commonly used a four-location version of the SRT task with a 12-item second-order conditional (SOC) sequence coupled with a test of explicit knowledge (e.g. Exner, Koschack, & Irle, 2002; Kelly & Burton, 2001; Reber & Squire, 1998). SOC sequences are constructed so that the next stimulus can only be predicted by knowing the previous two stimuli. SRT and recognition tests are used in the present experiments to investigate whether participants who observe the responses of an expert model can learn a 12-item SOC sequence, and whether they are aware of any movement information learned through imitation.

It is a contentious issue whether participants can learn a 12-item SOC sequence through observation in an SRT task. While clear evidence of observational sequence learning has been provided by Heyes and Foster (2002) and the experiments reported in Chapter 2, these experiments used a 6-item unique sequence. Several experiments
have found differences between learning of sequences in which transitions are simple (as in a unique sequence), compared to sequences with a more complex structure (such as SOC sequences). These differences include; a greater effect of dual tasks (Cohen, Ivry, & Keele, 1990 experiments 3 and 4), and age (Howard & Howard, 1997; 2001), on learning of complex sequences, a positive effect of the intention to learn on simple but not complex sequences (Curran & Keele, 1993), and most importantly for this study - that observational sequence learning is more likely to occur for short, simple sequences (Howard, Mutter, & Howard, 1992).

Using a 12-item SOC sequence, Kelly and Burton (2001) compared the ability of observers to learn the sequence with that of participants who practiced the sequence by responding to stimuli during training. In the first of their experiments, observers watched a practice participant complete the training blocks. On test, practice participants demonstrated implicit sequence knowledge while observers did not demonstrate sequence knowledge on either the SRT test, or on a generation test of explicit knowledge. A non-spatial version of the SRT task was used in Kelly and Burton's second experiment. Instead of spatial location, the colour of a centrally-located circle signalled the correct response. In this study observers watched stimulus presentation only; responses to the stimuli were not observed. Results from the second experiment matched those of the first: practice participants showed implicit learning of the sequence, while observers did not show learning on any test. Kelly and Burton (2001) concluded that observational learning in the SRT task is necessarily explicit and is therefore not shown when sequence properties encourage implicit learning.
Kelly, Burton, Riedel and Lynch (2003) found evidence supporting this conclusion when they compared sequence knowledge gained through observation of screen stimuli with that gained through physical practice and manipulated participants' awareness of the sequence. Half of the participants in each group were trained using the normal SRT task, and the other half were trained on sequences which had been broken up into triplets through the use of colour. It was expected that making the sequence more salient through the use of colour would lead to greater levels of explicit knowledge. Upon test, sequence knowledge was shown by both of the practice groups, but only by observers who had explicit knowledge of the sequence due to the colour manipulation. Thus, practice participants were able to learn the sequence implicitly but observers were not.

Two further experiments provide support for Kelly and Burton's claim that sequences cannot be learned implicitly through observation. Howard et al (1992) found sequence knowledge gained by observation of screen stimuli to be highly explicit and equivalent to physical practice on SRT and free generation tasks. A replication of this study showed that observational learning was only shown by those participants who exhibited high levels of explicit knowledge about the sequence (Willingham, 1999). In addition to these studies, an experiment using the sugar production task, a task which has been argued to be analogous to the SRT task (Kelly & Burton, 2001), found that observation could support learning of a salient, explicit rule, but action was necessary in order to learn the non-salient, implicit rule (Berry, 1991).

Although the majority of studies suggest that implicit learning is not possible by observation, Seger (1997) claims to have shown implicit observational learning using
the SRT task. Seger compared learning and awareness after either practice or stimulus observation of a 10-item sequence. Testing revealed that observers had gained as much sequence knowledge as practice participants. For a subset of observers who demonstrated low explicit knowledge by verbal report, learning was implicit as measured by recognition tests.

The purposes of the experiments reported in Chapter 1 were to 1) establish whether participants can learn a 12-item SOC sequence through observation of a model’s responses; 2) compare the amount of sequence knowledge gained through observation of stimuli alone, observation of stimuli and responses, and physical practice, and 3) investigate how aware participants are of any sequence knowledge gained through training.

3.1 Experiment 4

Experiment 4 investigated whether observers could learn a 12-item SOC sequence in comparison with untrained controls using the SRT task. An untrained control group was thought to be appropriate as the only experiment to assess observational learning of a 12-item SOC sequence (Kelly and Burton, 2001) found no sign of observational learning (even when observers were compared to untrained control participants on a generation test). Thus, this experiment sought to identify any effect of observational learning by comparing observers with participants who had no opportunity to learn the sequence.
Experiment 4 tested for observational sequence learning using parameters which have been shown to encourage implicit practice-based learning. If observational sequence learning is demonstrated, these parameters will be used to assess how aware participants are of any sequence knowledge gained through observation in Experiment 5. For this reason, a 12-item SOC sequence was used as the training sequence. The majority of studies which have reported implicit practice-based learning have used 12-item SOC sequences (e.g. Exner, Koschack, & Irle, 2002; Kelly & Burton, 2001; Reber & Squire, 1998).

Two types of observational training were given in this experiment. Participants either viewed stimulus presentation, or viewed both stimulus presentation and the responses of an expert model. By definition, imitation learning consists of learning by observation of a model’s responses, rather than of the stimuli guiding those responses. However, experiments on observational sequence learning typically ask participants to view stimuli in the absence of a model’s response. Both observer groups are included here in order to 1) increase the relevance of these experiments to the existing literature on observational learning, and 2) as comparison of the two groups with respect to observational learning (Experiment 4) and awareness of knowledge (Experiment 5) may reveal theoretically important differences between learning through imitation, and learning through observation of inanimate stimuli.

The influence of the amount of training given to participants was also investigated; half of each observation group were presented with 64 sequence cycles during training, while the remaining participants were presented with 96. Thus, the experiment consisted of a familiarisation phase in which all participants physically
responded to one block of the SRT task with random stimulus presentation in order to
gain task practice without being exposed to the training sequence. Training, which
followed the familiarisation phase, was completed according to group membership.
Participants in Group Observe Screen watched stimuli which followed the training
sequence in the absence of any response. Participants in Group Observe Screen and
Hands watched an expert model complete the usual SRT task and were instructed to
pay equal attention to stimulus presentation and the model's responses. Control
participants completed anagrams for a similar period of time. Sequence knowledge
was tested using the SRT test. In one block stimulus presentation was governed by the
training sequence and in a second block by a different 12-item SOC sequence. An RT
increase upon transference to the new sequence was used as an index of learning. If
this increase is greater in observers than in control participants, then observational
learning has been demonstrated.

3.1.1 Method

Participants. Seventy-two students at UCL participated in the experiment, 24 in each
of groups Observe Screen, Observe Screen and Hands, and Control. Their mean age
was 23 years, 37 were male, and each was paid a small honorarium for their
participation. Twelve participants who made more than 10% errors during the
random and test blocks were replaced.

Stimuli & Apparatus. Stimulus presentation, RT measurement, and response
recording were all implemented on IBM-compatible PCs with 43 cm colour monitors
and standard QWERTY keyboards. Four boxes were presented in a horizontal row in
the centre of the screen, drawn with black lines against a grey background. The boxes
were 2.2 cm wide and 1.2 cm high, spaced 1-cm apart, and viewed at a distance of approximately 60 cm. A white asterisk (Arial font size 36, subtending approximately 0.5° of visual angle) appeared in the centre of one of these boxes on each target location trial. Target locations are referred to as 1-4 from left to right. Participants were instructed to indicate locations 1-4 as quickly as possible by using the V, B, N, and M keys located across the bottom of the keyboard, respectively. They operated the V and B keys with the ring, and index fingers of their left hand, and the N, and M keys with the index, and ring fingers of their right hand, respectively.

Each test block consisted of 96 target location trials. Half of the participants in each group were trained with blocks consisting of 96 trials, and the other half were trained with blocks of 144 trials. Incorrect responses were signalled by a tone. A trial ended when a participant pressed the correct key, at which time the target was erased. The next trial began 200 ms later. Response latencies were measured from the onset of the target to the completion of a correct response.

Procedure. Participants were told that they were taking part in a choice RT task designed to measure their speed of response. For all participants, the experiment had three phases: 1) familiarization, 2) training, and 3) testing. The three groups received identical treatment in all phases except the training phase. During training, Group Observe Screen and Hands (OS+H) watched the experimenter's fingers as she performed the SRT task, and also observed stimulus presentation i.e. the asterisk moving between the on-screen boxes. Group Observe Screen (OS) watched stimulus presentation only; the experimenter did not make responses. In order to approximately equate the inter-stimulus interval (ISI) between the two observation groups, the ISI
was set at 500ms for Group Observe Screen. This duration is made up of the standard length between a response and the next trial on test blocks (200ms) plus the experimenter’s target RT for training blocks given to Group OS+H (300ms). Group Control (C) completed anagram problems for a comparable period of time.

Familiarization. In the familiarization phase, participants were asked to complete one block of 96 target location trials in which the order of target presentation was randomly determined.

Training. Group OS+H were instructed to watch the experimenter's fingers, and the movement of the stimulus on the screen, as she completed eight blocks of target location trials. Participants were asked to pay equal attention to the screen and the experimenter’s fingers. The sequence of targets in these blocks was 2-4-2-1-3-4-1-2-3-1-4-3, a 12-item second-order conditional sequence. Each block of 96 or 144 trials included eight or 12 repetitions of the whole training sequence, and began at a random point in that sequence. Observers in group OS+H were seated to the right, and just behind the experimenter, on a chair which had been raised to give them a slightly elevated view of her fingers on the keyboard. The screen was turned slightly towards the observers so that they could see the target stimuli to which the experimenter was responding. The experimenter provided a model of expert performance, with a mean RT over all experiments of 330ms and an average error rate of less than 1%. Participants in Group OS were seated in front of the computer and were asked to watch the screen as the asterisk moved between stimulus locations. Asterisk presentation was governed by the same sequence as used for Group OS+H. For the
duration of the training period (9 minutes), participants in Group Control solved anagram problems.

Testing. The test of sequence learning consisted of two blocks of target location trials, completed by all participants. In the first of these blocks, targets were presented in the training sequence, i.e. 2-4-2-1-3-4-1-2-3-1-4-3. In the second block, they were presented in a new, 12-item SOC sequence: 2-4-1-3-2-1-4-2-3-4-3-1.

3.1.2 Results and Discussion

A mean RT for each participant in each block was calculated after exclusion of RTs greater than 1000ms. Each analysis of RT data was accompanied by a parallel analysis of error data. The results of error analyses are reported only if they yielded significant effects or interactions. For all analyses, all significant effects are reported.

Initially results were analysed including amount of training (64 or 96 sequence cycles), as a between-subjects factor. However, this factor did not interact significantly with any other factor, nor was it significant as a main effect in any analysis. Therefore, this variable was not included in the reported analyses.

Data from the initial familiarization stage were analysed using univariate ANOVA with group (OS+H, OS, and C) as a between-subjects factor. The effect of group was not significant (F < 1), indicating that groups did not differ in their RT to random stimuli (Group OS+H M = 453 SEM = 14, Group OS M = 451 SEM = 15, Group C M = 450, SEM = 13).
In order to assess sequence knowledge on test, RTs in the training and new sequence blocks were compared. Mean RTs for each group on each block are shown in Figure 6. These data were analysed in the same manner as those in Chapter 2; a difference score was calculated for each participant by subtracting their RT on the sequence with which they were trained, from their RT on the new sequence block. These difference scores were then analysed using univariate ANOVA with group (OS+H, OS, and C) as a between-subjects factor. This analysis was supplemented by a Helmert contrast, comparing the control group to the two observation groups, and then Group OS+H with Group OS. The main effect of Group was significant \( F(2,69) = 3.7 \) p = 0.031, as was the contrast between the control (\( M = -10 \text{ms} \) SEM = 5) and observation groups (p = 0.01). The contrast between Group OS+H (\( M = 30 \text{ SEM} = 15 \)) and Group OS (\( M = 21 \text{ SEM} = 11 \)) was not reliable.

Figure 6 – Mean RT to training and new sequenced blocks for groups that; observed screen stimuli and the model's responses (Observe Screen and Hands), observed screen stimuli alone (Observe Screen), or completed anagram problems (Control), during training in Experiment 4.
Thus, the results of Experiment 4 demonstrated that observers are able to learn a 12-item SOC sequence. In addition, they suggested that the extent of learning did not vary between a group which observed the model's responses as well as the on-screen stimuli, and a group which observed the on-screen stimuli alone. Furthermore the amount of training (64 vs. 96 sequence cycles) did not affect the amount of sequence knowledge shown on test.

3.2 Experiment 5

Experiment 4 indicated that a 12-item SOC sequence can be learned by observation. Experiment 5 compared the amount of sequence knowledge gained through observation, with that gained through physical practice. To this end, groups trained by observing the onscreen stimuli only (Group OS), and the onscreen stimuli and an expert model's responses (Group OS+H), were compared to a practice group (Group P) which responded to onscreen stimuli. These groups were compared to an untrained control group. An untrained control group was used in Experiment 5 in order to provide a baseline from which both observational and practice-based learning could be measured. The alternative would have been to include 3 control groups: one of which responds to random stimuli in the training phase, one group which observes random stimuli in the training phase, and another which observes random stimuli and the responses of an expert model to those stimuli. This strategy would have made comparison of observational and practice-based learning problematic.
Observers were compared with practice participants in an attempt to explain conflicting results in the preceding literature and to test a revised version of the claim by Kelly and Burton (2001) that action is necessary for implicit learning. Two recent experiments have compared observational and practice-based learning in the SRT task and obtained very different results. Kelly and Burton (2001) found significantly less learning of a 12-item SOC sequence when observers were compared to practice participants. In contrast, Heyes and Foster (2002) found equivalent observational and practice-based learning of a six-item unique sequence. A possible explanation for these conflicting results is that differences in structure and length between sequences used in the studies may have resulted in differing amounts of observational learning. Howard, Mutter and Howard (1992) have shown that observational sequence learning is more likely to occur when sequences are short and have a simple structure. Thus, the use of a six-item unique sequence in the study by Heyes and Foster (2002) would have resulted in high levels of sequence knowledge, while the 12-item SOC sequence used by Kelly and Burton (2001) would result in less learning. This hypothesis was indirectly tested in Experiment 5 by comparing observational and practice-based learning of a 12-item SOC sequence. If practice and observer participants only showed equivalent learning due to the use of a short, simple sequence in Heyes and Foster (2002), one would not expect these groups to show equivalent learning in Experiment 5.

In addition to a test of sequence knowledge, recognition tests were performed in order to establish participants' awareness of any sequence knowledge gained through training. Experiments in this chapter are concerned with determining whether learning through imitation can be implicit. Results of Group OS+H, trained by observation of
an expert model’s responses and screen stimuli, will provide an initial answer to this question. The performance of the stimulus observation and practice groups will enable the following hypothesis to be tested.

Kelly and Burton (2001) have argued that action is necessary to learn implicitly, basing this claim on the large number of studies to demonstrate implicit practice-based learning (e.g. Exner, Koschack, & Irle, 2002; Kelly & Burton, 2001; Reber & Squire, 1998), and studies which suggest that observers cannot learn implicitly (e.g. Berry, 1991; Howard et al, 1992; Kelly and Burton, 2001; Kelly et al, 2003; Willingham, 1999). However, theories of imitation argue that observation of an action causes that action to be primed in the observer (see section 1.3.1.1 of Chapter 1 for evidence). Thus, one would expect that observation of a model’s response in the SRT task would produce the same type of knowledge as that gained through physically responding. If this is true, then observation of a model’s responses, in common with practice-based knowledge, may lead to implicit learning. Observation of screen stimuli however would still be expected to rely on explicit knowledge. It is interesting to note that all of the experiments which have shown observational learning to rely on explicit knowledge have trained observers with screen stimuli, but not with a model’s responses. If the above hypothesis is true, one would expect the performance of Group OS, and Group OS+H to differ on the recognition test. Group OS, which have not been trained using a model’s responses, should have no opportunity to learn implicitly if action is necessary for such learning. In contrast, Group OS+H are trained by observing a model’s response, and if action observation causes motor activation, would have the opportunity to learn implicitly. Comparison of Group OS+H with Group P will enable the claim that action is necessary for implicit
learning to be assessed. As both groups are trained on the same number of sequence cycles, and both groups have access to action representations of the sequence (directly for Group P and through observation of a model’s response for Group OS+H), one would expect Group OS+H to show implicit learning if Group P learn implicitly.

3.2.1 Method

The method was exactly the same as that of Experiment 4, except as noted.

Participants. An additional forty-eight volunteers participated in Experiment 5. These were randomly allocated to four equal groups: Observe Screen (OS), Observe Screen and Hands (OS+H), Practice (P) and Control (C). Their mean age was 23 years, 15 were male, and each was paid a small honorarium for their participation. Two participants who made more than 10% errors during the random and test blocks were replaced.

Procedure. In Experiment 4 the number of sequence cycles presented to participants during training (64 or 96) did not affect the magnitude of learning. Therefore participants in Experiment 5 were trained with an intermediate number of sequence cycles, i.e. 80. The training procedure for Group OS+H, Group OS, and Group C was the same as in Experiment 4. Group P were asked to respond to training blocks in the same manner as test blocks using the same keys and fingers. Participants in Group P were seated approximately 60cm in front of the computer screen, so that their visual experience of the onscreen stimuli was the same as that of Group OS.
Recognition Test. Following training and initial testing, participants were given a recognition test. The recognition test used in this experiment was the same as that used in Experiment 2 of Chapter 2, but was adapted for a 12-item sequence with four response locations. Participants were told that they would be given sequences of six asterisk locations, presented in the usual stimulus array. They were to respond to these stimuli as they had during familiarization and initial testing, using keys V-M, operated by the index and middle fingers of each hand. After responding to the sequence of six stimulus presentations, they were asked to give a rating of how confident they were that the test sequence was the same as the sequence used during training and initial testing. As before, ratings were made on a scale from 1 to 6, where 1 = certain I have not seen the sequence before, 2 - fairly certain I have not seen the sequence before, 3 - guess I have not seen the sequence before, 4 - guess I have seen the sequence before, 5 - fairly certain I have seen the sequence before, and 6 - certain I have seen this sequence before. Both ratings and trial-by-trial RTs were recorded. There were 12 test sequences in total, presented in random order. Six 'old' sequences were derived from the training sequence, and six 'new' sequences were derived from the sequence: 2-4-1-2-1-3-4-2-3-1-4-3. New test sequences were selected which did not occur in the training sequence.

3.2.2 Results and Discussion

Data from the familiarization stage were analysed as in Experiment 4, using univariate ANOVA with group (OS+H, OS, P, and C) as a between-subjects factor. The effect of group was not significant (F< 1), indicating that groups did not differ in
response time to random stimuli (Group OS+H Mean = 418 SEM = 17, Group OS M = 465 SEM = 22, Group P M = 430 SEM = 20, Group C M = 440 SEM = 21).

As in Experiment 4, sequence knowledge was calculated using a difference score which reflects any difference in response speed to the training and new sequences. These data (shown in Figure 7), were entered into a univariate ANOVA with group (OS+H, OS, P, and C) as a between-subjects factor. The effect of group was significant ($F_{(3,44)} = 4.4, p = 0.009$). A Helmert contrast compared control with experimental (OS+H, OS, and P) groups in the first instance, then practice with observation groups, and finally the two observation groups. This analysis revealed a significant difference between the control and experimental groups ($p = 0.002$), no difference between the practice and observation groups, and no difference between the two observation groups.

![Figure 7](image.png)

Figure 7 – Mean RT to training and new sequenced blocks for groups that; observed screen stimuli and the model's responses (Observe Screen and Hands), observed screen stimuli alone (Observe Screen), responded to stimuli (Practice), or completed anagram problems (Control), during training in Experiment 5.
Results from the initial test indicate that groups OS+H, OS, and P learned more of the sequence than the control group. In addition the amount of learning shown by the observation groups was equal in magnitude to that of the groups which physically responded during training. No difference was found, as indexed by the amount of learning shown on the initial test, between observation of screen stimuli alone, and screen stimuli and the responses of the model.

Table 3 shows mean RT and rating data from both training and new test sequences presented in the recognition test. Analysis of the recognition test followed the same format as in Experiment 2. Separate analyses were performed on the RT and rating data to identify sequence knowledge shown by any group on each measure. Analysis of the RT data was completed using ANOVA with sequence (training, new) as a within-subjects factor, and group (OS+H, OS, P and C) as a between-subjects factor. The analysis revealed a significant main effect of sequence ($F_{(1,44)} = 34.4 p < 0.001$), but not of group ($F_{(3,44)} < 1$). The interaction between sequence and group was not reliable ($F_{(3,44)} < 1$). Simple effects analysis (warranted by Howell 1996, p. 415) revealed that there was a significant difference in RT to training and new sequences for Groups OS+H ($F_{(1,44)} = 16.9 p < 0.001$), OS ($F_{(1,44)} = 9.8 p < 0.003$), and P ($F_{(1,44)} = 7.9 p < 0.007$). The difference in RT between training and new sequences for the control group was not reliable ($F_{(1,44)} = 2.9 p = 0.098$).
Table 3. Mean (+- standard error) RT and recognition ratings given to training and new sequences by groups that had observed screen stimuli (Observe Screen), observed screen stimuli and model’s responses (Observe Screen & Hands), responded to stimuli (Practice), or completed anagrams (Control) during training in Experiment 5.

The same ANOVA applied to the rating data revealed a significant main effect of sequence ($F_{(1,44)} = 19.0 \ P < 0.001$), but neither the main effect of group ($F<1$), nor the sequence by group interaction ($F_{(3,44)} = 2.0 \ p = 0.125$) was reliable. Simple effects analysis demonstrated that training sequences were rated as significantly more familiar than new sequences by groups, OS ($F_{(1,44)} = 17.6 \ p < 0.001$), and P ($F_{(1,44)} = 4.6 \ p = 0.038$), but not by groups OS+H and Control ($F_{(1,44)} = 1.8 \ p = 0.184$, and $F_{(1,44)} = 1.0 \ p = 0.311$, respectively).

Thus, in the recognition test Groups OS and P showed sequence knowledge as indexed by RT and ratings of familiarity, indicating that their sequence knowledge was explicit. Group OS+H exhibited sequence knowledge on the RT measure but not on the rating measure, suggesting that their sequence knowledge was implicit. The control group did not show any sequence knowledge on either the RT or rating measures. It must be noted at this stage that although the results of Group OS+H demonstrate implicit learning based on the standard interpretation of this type of recognition test (e.g. Seger, 1997; Shanks & Johnstone, 1999), the claim rests on a
null effect; that there is no statistically significant difference in the recognition ratings given to training and new sequences by Group OS+H. Such a null result does not justify a strong claim of implicit learning in Group OS+H: the difference between ratings given to training and new sequences may become statistically significant using other methods of statistical analysis and/or given greater experimental power. The results of this test are still of some use however; although Group OS+H show a numerically greater amount of sequence knowledge, as indexed by a difference in mean RT to training and new sequences, than Group OS and Group P, the level of sequence knowledge revealed by recognition ratings is less for Group OS+H than Group OS and Group P. Thus, while not providing sufficient evidence to support a strong claim of implicit learning by Group OS+H, these results do suggest that the sequence knowledge acquired by Group OS+H was less available for conscious use than that acquired by Groups OS and P.

Experiment 5 replicated and extended the results of Experiment 4 in several important respects. First, the observational learning of a 12-item SOC sequence shown by Groups OS+H and OS in Experiment 4 was also shown in Experiment 5. Second, the extent of this learning was found to be comparable in magnitude to a group of participants who physically practised the task during the training period. Third, the results from the recognition test indicated that the sequence knowledge gained by the Observe Screen and Practice groups was explicit; but that the sequence knowledge gained by the Observe Screen and Hands group was less available to consciousness i.e. the results suggested that learning may have been implicit. It was suggested that a sequence of responses could be learned implicitly due to the reliance of implicit
learning on action, and the ability of human movement observation to produce motor activation. This hypothesis was tested further in Experiment 6.

3.3 Experiment 6

The results of Experiment 5 suggested that observational sequence learning by a group of participants who observe stimulus presentation only was explicit in nature. In contrast, results of the recognition test implied that the sequence knowledge gained through the observation of stimuli and the responses of an expert model may have been implicit. There are at least two potential reasons for this contrast: observation of a model's actions and observation of screen stimuli may lead to different types of learning, or to different amounts of learning of a single type.

The former explanation assumes that learning a sequence of observed body movements is qualitatively different to learning a sequence of screen stimuli. Evidence consistent with this assumption includes studies reporting activation of cortical and periphery motor neurons in response to observation of biological, but not inanimate, movement stimuli (e.g. Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Manthey, Schubotz, & von Cramon, 2003; Stevens, Fonlupt, Shiffrar, & Decety, 1999; see Chapter 1 section 1.3.1.3 and 1.3.1.4). These data suggest that observation of the model's responses in addition to stimulus presentation may have resulted in different cortical processing compared to the observation of stimulus presentation alone. Such a distinction between learning of human movements and inanimate stimuli is consistent with the three theories of imitation tested in this thesis.
The second explanation, that observation of the model’s response distracts attention from observation of the screen stimuli and thus sequence knowledge does not become explicit, is consistent with data showing that increasing training can result in implicit knowledge becoming explicit (Frensch & Runger, 2003; Remillard & Clark, 2001; Seger, 1997). This explanation assumes that observation of the model’s response does not contribute to sequence knowledge.

To distinguish between the qualitative and quantitative possibilities, Experiment 6 presented participants with stimuli in which hand movements were the sole source of information (Group Observe Hands). Participants observed the model’s responses but were prevented from viewing the stimuli to which the model was responding. If the Observe Screen and Hands group learned implicitly in Experiment 5 as a result of observing movement stimuli, then this group should also learn implicitly. The control group in Experiment 6, as in Experiments 4 and 5, completed anagrams throughout the training period.

3.3.1 Method

Participants. An additional 24 volunteers participated in Experiment 6. These were randomly allocated to two equal groups: Observe Hands (OH), and Control (C). Their mean age was 27 years, 15 were male, and each was paid a small honorarium for their participation. Three participants who made more than 10% errors during the random and test blocks were replaced.
Procedure. The procedure of Experiment 6 was exactly the same as Experiment 5 except as noted. The treatment of Group OH during training was the same as that of Observe Screen and Hands in Experiment 5, except that the computer screen presenting stimuli to the expert model was rotated approximately 60° away from the participants. This meant that participants could not see stimuli being presented. They were asked to pay attention to the model’s hands as she completed the training blocks. The treatment of the Control group was the same as in Experiment 5.

3.3.2 Results and Discussion

Data from the familiarization stage were analysed using univariate ANOVA with group (OH and C) as a between-subjects factor. The effect of group was not significant ($F(1,22) = 1.4 \ p = 0.245$), indicating comparable RT to random stimuli between Group OH ($M = 517 \ SEM = 19$) and Group C ($M = 485 \ SEM = 19$).

RT on test blocks to training and new sequences are shown in Figure 8. Difference scores derived from RTs to the training and new sequenced blocks were entered into a univariate ANOVA with Group as a between-subjects factor. The difference between Group OH and C was significant ($F(1,22) = 5.2 \ p = .033$).
Data from the recognition test are shown in Table 4. Analysis of the RT data from the recognition test revealed significant main effects of sequence ($F_{(1,22)} = 20.4 \ P < 0.001$), and group ($F_{(1,22)} = 14.4 \ P = 0.001$). The interaction between sequence and group was also significant ($F_{(1,22)} = 9.4 \ P = .006$). Simple effects analysis indicated that in Group OH RTs to new sequences were significantly longer than RTs to training sequences, and that for Group C RTs to new and training sequences did not differ.
Table 4. Mean (+- standard error) RT and recognition ratings given to training and new sequences by groups that had observed a model's fingers as he responded to the training sequence (Observe Hands) or had completed anagram problems (Control) during training in Experiment 6.

<table>
<thead>
<tr>
<th>Group</th>
<th>Mean Rating Training (SEM)</th>
<th>Mean Rating New (SEM)</th>
<th>Mean RT Training (SEM)</th>
<th>Mean RT New (SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observe Hands</td>
<td>3.86 (0.18)</td>
<td>3.46 (0.35)</td>
<td>513 (26.4)</td>
<td>571 (33.6)</td>
</tr>
<tr>
<td>Control</td>
<td>3.86 (0.21)</td>
<td>3.67 (0.12)</td>
<td>411 (15.4)</td>
<td>422 (15.1)</td>
</tr>
</tbody>
</table>

The same analyses applied to the recognition rating data did not show any significant effects in either the initial ANOVA (Sequence F(1,22) = 2.7 p = 0.115, Group, Sequence x Group Fs < 1), or subsequent simple effects analysis (Group OH F(1,22) = 2.4 p = 0.132, Group C F < 1).

Although interpretation of the recognition test rests on a null effect, and so implicit learning cannot be definitively claimed, this experiment demonstrated that observers of a model's response can learn a 12-item SOC sequence and suggested that they may not have been aware of their sequence knowledge. These results, in combination with the results of Experiment 5, suggest that observation of action may lead to learning which is qualitatively different from that gained through observation of inanimate stimuli. Furthermore, these results suggest that observation of a movement sequence may support implicit learning.
3.4 General Discussion

Experiment 4 demonstrated that both observers of stimuli, and observers of stimuli plus the responses of an expert model, could learn a 12-item SOC sequence in an SRT task. Sequence knowledge gained by these groups through observational training was greater than that of untrained controls. Experiment 5 replicated and extended this result by confirming that participants who receive observational training learn more than untrained participants, and that observers learn as much as participants who physically respond to stimuli during training. Interestingly, the results of the recognition test indicated that sequence knowledge gained by the Observe Screen and Practice groups was explicit, but knowledge gained by the Observe Screen and Hands group may have been implicit in nature. Experiment 6 showed that observers of a model’s response without screen stimuli were able to learn a 12-item SOC sequence. In addition, results of the recognition test suggested that participants were unaware of sequence knowledge they had gained through training.

The finding that a 12-item SOC sequence can be learned through observation, and that the magnitude of such learning is comparable to physical practice, conflicts with the results of Kelly and Burton (2001). Kelly and Burton found no evidence of observational learning in comparison with practice participants. However, the present findings support those of Seger (1997) and Heyes and Foster (2002) who found equivalent learning by observation and physical practice using 10 and 6-item sequences, respectively.

Possible reasons for the contrast between the results of Kelly and Burton (2001) and those obtained in these experiments may lie in the details of what participants
observed in the two studies. In the first of Kelly and Burton's experiments, observers watched screen stimuli and the responses of a novice responder. This group can be compared with Group Observe Screen and Hands in the present experiments, in which participants also had the opportunity to observe screen stimuli and responses. The most apparent difference between the two sets of experiments is the level of expertise of the model. The present experiments used an expert model who responded at a constant rate and who made very few errors. In contrast, responses observed in Kelly and Burton's first experiment were made by a novice participant, who would have presumably made more errors, and produced less fluid movements than an expert model. Response errors would mean that the sequence is disrupted and thus would become probabilistic; instead of the stimuli appearing according to the sequence 100% of the time, the probability of a sequential response would be lower. Research which has investigated the effect of training on probabilistic sequences has suggested that learning proceeds at a slower rate with small amounts of sequence uncertainty, and does not occur at all with increased rates of uncertainty (Schvaneveldt & Gomez, 1998).

In the second of Kelly and Burton's (2001) experiments, participants observed stimulus presentation only and thus were comparable to the Observe Screen group in the present experiments. Kelly and Burton did not find any evidence of observational learning in comparison with participants who responded during training, but Observe Screen participants in the present experiments showed comparable learning to practice participants. A potential reason for this difference in results is that Kelly and Burton's participants observed a non-spatial sequence while a spatial sequence was observed in the present experiments. It is possible that observational learning of screen stimuli is
more likely to occur when spatial stimuli are used. Evidence consistent with this hypothesis is that studies reporting observational sequence learning of screen stimuli in the SRT task have all used a spatial sequence (e.g. Howard et al, 1992; Kelly et al, 2003; Seger, 1997; Willingham, 1999). Also, these experiments find that observers learn the sequence explicitly (although Seger, 1997 reports implicit learning shown by a subset of observer participants), and Hikosaka et al (2002) have argued that explicit learning in sequence tasks is mediated by spatial knowledge. Thus it is plausible that Kelly and Burton (2001, exp. 2) failed to find observational learning due to the use of a non-spatial sequence.

The suggestion that observational learning may have been implicit is perhaps the most significant of these experiments, both for the preceding literature and for theories of imitation. It has been argued that observational learning must be explicit; that action is necessary in order to learn implicitly (Kelly & Burton, 2001). Experiments supporting this claim include Kelly et al (2003), Howard, Mutter, and Howard (1992), Willingham (1999) and Berry (1991). These experiments have all demonstrated the reliance of observational learning on explicit knowledge. Results of the Observe Screen group in the present experiments support this view: The Observe Screen group learned the sequence by observation and showed awareness of this knowledge on the recognition test. However, results of the group which observed screen stimuli and a model’s responses (Observe Screen and Hands), and the group which only observed the model’s responses (Observe Hands) indicate that participants in these groups may have learned implicitly. These groups both learned through observation but did not reliably rate training sequences as more familiar than new sequences.
The hypothesised difference in awareness between the Observe Screen group and the groups that observed a model's response is striking, because all were exposed to the same amount of training on the same sequence. Two possible reasons for the different levels of awareness after observing responses and stimuli were proposed. The first was that observation of a model's response produces a different kind of learning and one of the features of this type of learning is that it can be implicit. The second suggests that learning goes through a transition from being implicit to explicit with increasing sequence experience. Observation of a model's response as well as screen stimuli may lead to distracted attention and reduce the amount of sequence experience compared to screen stimuli alone.

Experiment 6 was a first step in refuting the second explanation. Observed responses were the sole source of sequence information in Experiment 6, and yet results suggest observers may still have learned the sequence implicitly. However, the results of Experiment 6 do not rule out an explanation based on decreased sequence knowledge. They show that viewing the model's fingers is not merely a source of distraction; that observed finger movements are instead a source of sequence knowledge. However, it is still possible that observing finger movements provides less sequence information than observing screen stimuli, and therefore that the groups that observed finger movements failed to provide evidence of explicit knowledge because they had less information of the same kind as that of the Observe Screen group.

The finding that the Observe Screen and Observe Screen and Hands groups showed no difference in the magnitude of sequence knowledge upon initial testing in Experiments 4 and 5 argues against an explanation based on the amount of sequence
knowledge. This finding suggests that sequence knowledge was equal between the groups. Although it is possible that the rating measure on the recognition test detected a difference in sequence knowledge which the RT measure did not, this is unlikely due to the categorical 6-point nature of the rating scale compared to the continuous RT measure. An explanation resting on differential amounts of sequence knowledge between the groups would still run counter to Kelly and Burton’s (2001) claim that implicit observational learning cannot occur, as observational learning would have to be implicit in the early stages of training.

The alternative explanation, that observation of a model’s response produces a different type of learning, has support from preceding experiments and can be incorporated into Kelly and Burton’s hypothesis about the necessity of action for implicit learning. Evidence suggesting motor activation in response to action observation has been provided by neurological and neurophysiological experiments showing action observation leads to the activation of cortical and peripheral motor neurons (e.g. Aziz-Zadeh et al., 2002; Buccino et al., 2001; Hari et al., 1998). Behavioural evidence for this process has been provided by experiments demonstrating action priming in response to action observation including; Brass et al (2000, 2001), Stürmer et al (2000), Heyes and Foster (2002), and the experiments in Chapter 2.

These experiments suggest that learning may be qualitatively different when responses are observed as well as, or instead of, screen stimuli. Observers of responses may encode their sequence knowledge in a motoric fashion, as if they had responded during training. Observers who learn only screen stimuli have no
opportunity to engage in motor learning (as they neither respond, nor observe responses during training) and thus are unlikely to encode their sequence knowledge as motor representations.

This explanation is consistent with a recent theory of motor skill learning (Hikosaka, Nakamura, Sakai, & Nakahara, 2002) which describes the properties of two parallel learning processes. The first of these is concerned with the learning of motor information, information learned is effector-dependent (information learned with one effector cannot be transferred to another), and implicit (see also Russeler and Rosier, 2000). The second process is concerned with learning spatial information which is explicitly represented. Thus observers of a model’s responses may learn motor representations which are implicit, but observers of screen stimuli may learn a spatial sequence which is represented explicitly. It is significant that observers in all of the studies which have shown that observational learning relies on explicit knowledge have observed screen stimuli only (Howard, Mutter and Howard, 1992; Willingham, 1999; and Kelly et al, 2003). Furthermore, if observational learning of screen stimuli relies on spatial representations, this would explain why stimulus-observation participants in Kelly and Burton (2001) did not learn in a non-spatial task. This explanation may not be complete however. Participants who responded to stimuli in Experiment 5 did not learn implicitly, even though they would be the group expected to learn motor information. Previous studies have however, reported implicit learning in participants who respond to stimuli during training (e.g. Exner et al., 2002; Kelly & Burton, 2001; Reber & Squire, 1998), and results of Chapter 2 show that motor knowledge is not always implicit.
If the argument is accepted that observers of a model's response learned implicitly as they received some motor knowledge, then Kelly and Burton's (2001) claim that implicit observational learning is not possible must be modified. Implicit observational learning was ruled out due to a belief that action was necessary in order to learn implicitly. The results of this study suggest that motor representations may be necessary to learn implicitly, but that these can be gained from observation of movements. Thus, in combination with the results of Kelly and Burton (2001), the results of Experiments 4–6 suggest that implicit observational learning of a movement sequence may be possible, but implicit observational learning of a sequence of static, inanimate stimuli is not.

The implications of these results for theories of imitation are interesting. The AIM model of imitation argues that imitation is an effortful process which involves inference and an active comparison between current and desired body states. This model therefore implies that imitation of learned and novel behaviour will not be implicit. The present experiments investigated how aware participants were of information learned through imitation. The only groups in which imitative learning could have been demonstrated were the Observe Screen and Hands, and Observe Hands groups as these were the only groups trained through observation of a model's responses. The results showed that it was possible to learn a 12-item SOC sequence through observation of responses alone, and in combination with screen stimuli. The finding that these groups learned the sequence, but may have had no conscious awareness of what they had learned suggests that imitation was not accomplished according to the AIM model. In contrast, both the ASL and Ideomotor theories of
imitation posit that imitation can occur without awareness and are therefore consistent with the results of the present experiments.

In summary, Experiments 4 - 6 investigated the amount and nature of any sequence knowledge gained through observation in an SRT task. Learning due to observation of screen stimuli, screen stimuli and responses, and responses alone was compared to that due to physically responding to stimuli and a control group who completed anagram problems. Results revealed that all three observation groups could learn the sequence, and that observational learning was of equal magnitude to that gained through physical practice. Tests of awareness revealed that participants who responded to stimuli during training and those who observed screen stimuli were aware of the sequence knowledge they had gained. In contrast, results suggested that those participants who had observed either responses alone, or responses and screen stimuli, were unaware of their sequence knowledge, i.e. they had learned implicitly. If, as suggested by the present results, participants learned the sequence implicitly by observing a model’s response, then implicit learning through imitation is possible. Implicit imitation is not consistent with the AIM model of imitation described by Meltzoff and Moore (1977, 1994, 1997) but is consistent with both the ASL (Heyes, 2001; Heyes & Ray, 2000) and Ideomotor (Prinz, 1997, 2002) theories of imitation.
Chapter Four: The Role of Experience in Imitation

Theories of imitation suggest two main routes to imitative ability. AIM argues that an innate cognitive module is responsible for the ability to imitate, while ASL and Ideomotor theories attribute imitative ability to learned associations. ASL posits that these associations are between perceptual and motor representations. Ideomotor theory, in contrast, suggests associations are formed between actions and their effects (for further details see Section 1.2 of Chapter 1).

Experiments in this chapter investigated whether imitation is innate or experience-dependent by examining the impact of counter-imitative training on a movement compatibility effect. A movement compatibility effect is the name given to the finding that responses to movement stimuli are faster when stimulus and response movements match, than when they do not (see Section 1.3.1.1 of Chapter 1). It has recently been appreciated that the movement compatibility effect is a result of the imitation system (Brass, Bekkering & Prinz, 2001; Chapter 1; Prinz, 1997). Observation of an action primes the corresponding action in the observer; when the primed and response movements match, then responses are fast. However, when the primed and response movements do not match, then the primed response must be inhibited before the response movement can be performed.

Experiment 7 demonstrated a movement compatibility effect which was not confounded with spatial compatibility. Experiment 8 studied the effect of counter-imitative training on this movement compatibility effect. Counter-imitative training involves repeatedly pairing observation of a movement with the execution of an
incompatible movement. If imitation is achieved through a dedicated, innate, cognitive module, then one might expect modest amounts of counter-imitative training to have little effect on the movement compatibility effect. Conversely, if imitation is instead based on associative mechanisms in which experience is crucial, then the movement compatibility effect should be reduced or even reversed.

In summary. Movement compatibility effects are thought to rely on mechanisms used to produce imitative movements. In imitation, and in the movement compatibility effect, motor representations of perceived actions are activated. The aim of the experiments reported here is to discover whether movement compatibility effects can be modified through incompatible training. The susceptibility of the movement compatibility effect, and by association imitation itself, is of theoretical importance in the imitation literature.

4.1 Experiment 7

An example of an experiment which demonstrates a movement compatibility effect is that of Stürmer, Aschersleben and Prinz (2000). In this experiment a choice RT task meant that participants either opened or closed their hand in response to either hand opening or hand closing stimuli. Response selection (hand opening or closing) did not depend on which stimulus movement was observed, but instead on the colour of the movement stimulus. Stürmer et al found that responses were faster on compatible trials (where stimulus and response movements matched), than on incompatible trials (where stimulus and response movements were different).
Experiment 7 investigated whether a movement compatibility effect could be found using a procedure similar to that of Stürmer et al (2000). In a simple RT task, one of two response movements (either hand opening or hand closing) was performed in a blocked design. On each trial, the imperative stimulus was either an opening or closing hand, presented in random order on a computer screen. Thus, on every trial, stimulus and response movements were either the same, (compatible trials), or different, (incompatible trials). A simple RT task was used in order to increase the chances that the stimulus movement would be processed as a movement (rather than merely a change of colour), and thus increase the chances of a movement compatibility effect being found.

In order to preclude any confound of movement compatibility with simple spatial compatibility effects, stimulus and response movements were orthogonal. Stimulus movements were demonstrated with the arm in a vertical position (see Figures 9a and 9b). Response movements were perpendicular to stimulus movements about the vertical plane (across the body, see Figure 10). Orthogonal direction of stimulus and response movements is a departure from the procedure used by Sturmer et al (2000), who confounded spatial cues with movement type.

Figure 9a – Neutral (foreground), and Open movement end point (background)  
Figure 9b – Neutral (background) and Close movement end point (foreground)
Figure 10 – Position of the hand during stimulus (inset) and response movements. During stimulus movements the hand was arranged along the vertical axis (a), but along the horizontal axis (b) when participants were responding. The transverse horizontal axis (c) is also shown.

In an effort to reduce anticipation errors, the strategy of Brass, Bekkering and Prinz (2001) was adopted. Brass et al demonstrated movement compatibility effects in simple RT tasks and reduced anticipation errors by introduced a variable delay (800ms, 1600ms, or 2400ms) between the onset of the warning signal, and the onset of the imperative stimulus.
In line with previous reports of movement compatibility effects (e.g. Brass et al., 2001; Brass et al., 2000; Iacoboni et al., 2001; Iacoboni et al., 1999; Stürmer et al., 2000), it was expected that responding would be faster on compatible than on incompatible trials.

4.1.1 Method

Participants. Ten staff and students at UCL participated in the experiment. Their mean age was 33.6 years, two were male, all were right-handed, and each was paid a small honorarium for their participation. They all gave their informed consent to participate in the study.

Stimuli & Apparatus. Stimulus presentation was controlled by an IBM-compatible laptop (Dell Latitude C840) attached to a 38cm colour TFT display with a resolution of 1600 x 1200 pixels. Two hands were each digitally recorded performing the two stimulus movements (opening and closing), to provide two tokens of each stimulus movement type. Two movement tokens were used to increase the generality of results. The resulting videos were stored as AVI video files (1440 x 960 pixels) and played in colour on a black background (see Figure 9a, and 9b). The clips were edited so that opening and closing movements both started from a common neutral position, and the duration of each movement was 480ms. The common neutral frame for each model was used as a static warning signal for stimulus movement onset. All four video clips (two tokens of hand opening and two of hand closing), were played full screen. For hand closing, the final posture occupied approximately 10° of visual angle.
horizontally, and 13° vertically. For hand opening, the final posture occupied approximately 16° horizontally and 23° vertically. Viewing distance was approximately 60cm and the hands appeared slightly larger than life-size.

A second IBM-compatible laptop recorded two signals. One signal was the amplified EMG signal from the first dorsal interosseus muscle (FDI) and the second was a signal from the stimulus presentation program which marked the start and end of the stimulus movement. Comparison of these two signals allowed RT to the movement stimulus to be calculated, as both stimulus and response movement onsets were recorded.

Electromyographic Recording and RT Measurement. The movement of the right index finger, for both close and open responses, was measured by recording the electromyogram (EMG) from the first dorsal interosseus muscle of the right hand. Disposable Ag/AgCl surface electrodes (Arbo Inc., Stratford, CT, USA) were used. The right forearm of the participant (from elbow to wrist) was supported by an arm-rest. The EMG signals were amplified, high-pass filtered at 20 Hz, mains-hum filtered at 50 Hz and digitised at 2.5 kHz. The signals were recorded on a computer for later analysis. The EMG signal was rectified and smoothed using a dual-pass Butterworth filter, with a cut-off frequency of 50 Hz.

An algorithm was used to detect EMG onset for each trial. The algorithm used the standard deviation of the EMG signal during a baseline period of 95 ms before movement stimulus onset, and therefore prior to any EMG response, to estimate noise in the EMG signal. A criterion of 2.75 times this noise level was used to define
gesture onset. A window of 20ms was moved progressively over the raw EMG data in 1ms steps. When the standard deviation of the 20ms window, and the 20ms epoch occurring after the end of the window, both reached the criterion level, the beginning of the 20ms window was used as gesture onset time. This marked the end of the RT interval. Whether this criterion correctly defined gesture onset was verified by sight for every trial performed by every participant.

Participants were told which response movement to perform before each practice and test block. They were asked to perform each movement rapidly with a sudden movement onset, so that a clearly defined electromyographic signature signalling response movement onset would be produced. Visual feedback of the EMG signal produced by their movement was given to participants before practice blocks until they consistently produced movements which led to clearly defined muscle activity onset as illustrated by the EMG waveform. After completing one practice and two test blocks making one response movement, the process of EMG training was repeated for the alternative response movement. Visual feedback of the EMG waveform produced by participant’s activity was not provided during practice and test blocks.

Procedure. Participants were instructed to rest their right forearm on an arm-rest so that their hand was free to move. The arm was arranged horizontally (see Figure 10). Each trial began with the presentation of a static hand in the neutral starting position. The hand performed one of two stimulus movements, closing or opening, after one of three time delays (800ms, 1600ms, or 2400ms). Stimulus movement onset defined the start of RT measurement. A closing movement of the hand resulted in a fist being formed, while an open response ended with the fingers fully extended and spread.
apart (see Figure 9). The neutral resting posture, adopted by the participant between trials, was matched to the neutral starting posture shown on the movement stimuli videos, i.e. the hand was in a position halfway between the closed and open end-postures. Each movement started from the neutral resting position and the pre-instructed movement was executed as soon as stimulus movement was detected.

Participants were instructed not to move on catch trials (see below). After executing the response, the hand was returned to the neutral starting position. An experimenter, standing behind the participant, verified that the correct response was made and the hand was returned to the neutral starting position. At the end of each trial a blank screen was presented for one second. Thus, each trial consisted of the onset of the warning signal (static hand), a delay of 800ms, 1600ms, or 2400ms before onset of stimulus movement (duration 480ms). A blank screen was then presented for 1000ms (ITI) before the next trial began.

Participants completed a total of two practice blocks and four test blocks. Each test block was made up of 72 trials. Of these, 12 were catch trials in which the warning stimulus was not followed by the imperative stimulus, i.e. the static neutral hand position remained on screen without moving for 2880ms. The 60 remaining trials in each test block required the participant to make the pre-specified response to the onset of stimulus movement. These trials contained ten repetitions of each unique combination of stimulus movement (open or close) and stimulus onset asynchrony (SOA) factors. Movement token was counterbalanced across test blocks. Trials were presented in a random order. Test blocks were ordered so that participants completed two blocks of one response movement, either opening or closing, and then two blocks of the other. Although participants were asked if they would like to rest between test
blocks, none of them wished to do so. Order of test blocks (either open response followed by close response or vice versa) was counterbalanced across participants. One practice block preceded each set of two test blocks. Practice blocks were 12 trials long and were composed of two trials of each unique combination of the stimulus movement and SOA factors, with one of these unique combinations being randomly re-allocated as a catch trial.

4.1.2 Results and Discussion

RTs over 1000ms were excluded from the analysis. Movement errors (producing the wrong response or an absence of movement) did not occur in test blocks. On every trial, stimulus and response movements were either the same (compatible trials), or were different (incompatible trials). Thus, RT data were analysed using analysis of variance (ANOVA) with response (open, close), trial type (compatible, incompatible), Block (Block 1, trials 1-72, or Block 2, trials 73-144), and SOA (800ms, 1600ms, 2400ms) as within-subjects factors. In all analyses, all significant effects are reported (alpha = 0.05).

Figure 11 shows average (and SEM) RT on compatible and incompatible trials at each of the three levels of SOA. There was a significant main effect of trial type \( (F_{(1,9)} = 23.7 \ p = 0.001) \), and a significant main effect of SOA \( (F_{2,18} = 29.2 \ p < 0.001) \). On average, responding was 19ms faster on compatible trials (396ms SEM = 24) than on incompatible trials (415ms SEM = 27). At the two longest SOAs responding was faster than at the shortest SOA (435ms SEM = 23 at 800ms, 388ms SEM = 28 at 1600ms, and 394ms SEM = 27 at 2400ms). Although the compatibility effect was
numerically greater with an 800ms SOA, than a 1600ms or 2400ms SOA, the interaction between trial type and SOA was not significant ($F_{2,18} = 1.5 \ p = 0.249$).

![Figure 11](image)

**Figure 11** - Mean RT on compatible and incompatible trials at each level of SOA in Experiment 7. Outlined columns represent compatible trials and blocked columns represent incompatible trials. Vertical bars indicate SEM.

Experiments which have examined the relationship between response speed and the movement compatibility effect show a positive correlation between the two measures i.e. the movement compatibility effect increases as RT increases (Brass et al, 2001; Stürmer et al, 2000). To find out whether the magnitude of the compatibility effect varied with response speed in this experiment, the distribution of each participant’s compatible and incompatible RTs was separately divided into three bins (following Ratcliff, 1979). Compatible and incompatible trials could then be compared for slow, medium and fast responses. Mean RT on compatible and incompatible trials at each bin is presented in Figure 12. ANOVA with bin (fast, medium and slow responses)
and trial type (compatible, incompatible) as within-subjects factors revealed the following results: The main effect of trial type was significant ($F_{(1,9)} = 15.6, p = 0.003$), indicating that RT on compatible trials was faster than on incompatible trials. Trivially, the main effect of bin was also significant ($F_{(2,18)} = 45.4, p < 0.001$). The interaction between trial type and bin was not reliable ($F_{(2,18)} < 1$).

Experiment 7 demonstrated a movement compatibility effect with hand open/close movements under two novel conditions: First, in a simple RT task, and second, when stimulus and response movements are performed along orthogonal dimensions. Orthogonal stimulus and response movements preclude an explanation of the movement compatibility effect in terms of simple spatial compatibility. The present finding demonstrates that observing a specific movement (in this case opening or
closing of a hand), facilitates the performance of the observed movement. Thus it can be concluded, following previous researchers (e.g. Brass et al., 2001; Brass et al., 2000; Stürmer et al., 2000), that the movement compatibility effect indicates that perception of an action activates the motor representation of the perceived action in the perceiver. As the ability to activate the motor representation of a perceived action is a key feature of movement imitation, it is argued that the movement compatibility effect and imitation are products of the same functional mechanism.

4.2 Experiment 8

Experiment 8 investigated the effect of incompatible training on the movement compatibility effect. To my knowledge there are no previous studies which have investigated the effect of counter-imitative training on movement compatibility effects. However, related experiments have been performed in the field of spatial compatibility. Both spatial and movement compatibility effects are species of stimulus-response compatibility (SRC). SRC research investigates how characteristics of stimulus and response interact to affect performance. It has been argued that experiments on spatial compatibility are relevant to studies of imitation, and in particular to movement compatibility, as both are examples of SRC effects (Brass et al., 2001). In both cases perceptual input facilitates or inhibits the performance of a motor response.

Tagliabue, Zorzi, Umilta, and Bassignani (2000) attempted to change a standard spatial compatibility effect through incompatible training. Participants in an incompatible training group responded in a choice RT task in a spatially non-
corresponding manner i.e. a stimulus to the right of fixation was responded to with the left hand, and a stimulus to the left of fixation was responded to with the right hand. Participants then completed a Simon task in which they were instructed to respond to an outlined square with a right hand keypress, and a blocked square with a left hand keypress. The imperative stimuli appeared either to the left or the right side of fixation. It is typically found that spatially compatible responses are faster than incompatible in a Simon task, even though response selection is based on a non-spatial attribute (the ‘Simon Effect’). However, in this experiment, no Simon effect was found when spatially incompatible training was completed five minutes or 24 hours prior to training (see also Angrilli, Zorzi, Tagliabue, Stegagno, & Umilta, 2001; Tagliabue, Zorzi, & Umilta, 2002).

The experiments of Tagliabue and her colleagues provide good evidence that spatial compatibility effects can be eliminated or reversed through incompatible training. Experiment 8 utilised a similar design to these experiments. Participants completed the same test phase as those in Experiment 7. Testing was preceded by one of two types of training performed 24hrs prior to testing. Tagliabue et al (2000, 2001, 2002) have demonstrated that spatial compatibility effects can be negated with such a delay between training and test, and the delay may serve to lessen any confusion due to the difference in training and test task instructions.

Half of the participants received compatible training: they were required to execute response movements which matched stimuli movements presented on a computer screen. The remaining participants received incompatible training: they were instructed to respond to hand opening by closing their hand and to hand closing by
opening their hand. The amount of training (six blocks of 72 trials each) is towards
the lower end of a scale defined by the lowest and highest amounts of training in
which elimination or reduction of the spatial compatibility effect has been reported
(1800 trials - Proctor & Lu, 1999; 72 trials - Tagliabue et al., 2000).

If imitation is governed by an innate, hard-wired cognitive module (as in AIM), one
would not expect such relatively small amounts of incompatible training to have an
effect on the movement compatibility effect. However, if imitation is a product of
learning (as suggested by ASL and Ideomotor theories), then the movement
compatibility effect should disappear, or be reversed, after incompatible training.

4.2.1 Method

Participants. Twenty students at UCL participated in this experiment. Their mean
age was 23.25 years, eight were male, all were right-handed, and each was paid a
small honorarium for their participation. Participants gave their informed consent to
participate in the study, and were randomly allocated to one of two groups:
Compatible Training, or Incompatible Training.

Stimuli and Apparatus. These were the same as used in Experiment 7.

Procedure. The test procedure in Experiment 8 was exactly the same as that of
Experiment 7. Testing took place approximately 24hrs after training. Stimuli,
response movements, and methods of RT measurement in training blocks were the
same as in test blocks of Experiments 7 and 8. Training consisted of six blocks of 72
trials each. Training blocks followed the same format as test blocks, except that the delay between the appearance of the warning signal (static hand) and the imperative signal (start of hand movement) remained constant at one second. Catch trials were not included in training blocks and stimulus movement presentation was randomly determined on each trial. A choice RT procedure was used to train participants. Group Compatible Training (CT) was asked to respond with hand opening to opening of the stimulus hand, and with hand closure to closing of the stimulus hand. Group Incompatible Training (IT) was asked to respond by closing their hand when the stimulus hand opened and by opening their hand when the stimulus hand closed. In order to encourage accurate performance, the number of movement errors (both absent and incorrect responses) made by the participant was displayed after each training block. Participants were informed that if they reduced the numbers of errors they made in the next block (or maintained performance if error-free), they would receive a small financial reward. Participants were not made aware of the existence of this incentive scheme until after they had completed the first block.

A practice block was completed before training blocks. The practice block was structurally the same in every respect as that in Experiment 7 (with constant SOA), but responses were governed by group membership as indicated above.

4.2.2 Results and Discussion

Training. RTs over 1000ms were excluded from the analysis. Movement errors (as defined above) occurred in less than 0.1% of trials and therefore these data will not be
reported further. A mean RT was calculated for each participant for each training block.

Mean RTs for both groups in each training block are presented in Figure 13. Training data were analysed using ANOVA with block (1-6), as a within-subjects factor and group (CT or IT) as a between-subjects factor. Mauchly's Test indicated that the data significantly violated the assumption of sphericity ($W(i_{14}) = 0.051 \ p < 0.001$), and therefore ANOVA values were corrected using the Greenhouse-Geisser method. Significant main effects of training block ($F(5) = 16.45 \ p < 0.001$), and group were found ($F(1,18) = 22.49 \ p < 0.001$). The interaction between training block and group was also significant ($F(5,90) = 3.15 \ p = 0.045$). Between the first and the sixth block of training, RT decreased by 105ms (SEM 25.7) in group IT, and by 58ms (SEM 10.9) in group CT.

![Figure 13](image)

**Figure 13** – Mean RT for each training block in Experiment 8. Squares represent Group Compatible Training (CT) and triangles represent Group Incompatible Training (IT).
Test. No movement errors were made in any test block by any participant. Mean (and SEM) RT for both groups on compatible and incompatible trials are shown below in Figure 14. RT data were analysed using ANOVA with response (open, close), trial type (compatible, incompatible), Block (1 or 2), and SOA (800ms, 1600ms, 2400ms) as within-subjects factors, and group (CT or IT) as a between-subjects factor. The analysis revealed a significant main effect of trial type ($F_{(1,18)} = 23.1 \ p < 0.001$), and a significant main effect of SOA ($F_{(2,36)} = 26.4 \ p < 0.001$). On average, compatible movements were executed 21ms faster than incompatible movements, and responses following the two longest SOAs were executed faster than those made after the shortest SOA (RT 401ms at 800ms SOA, 368ms at 1600ms SOA, and 375ms at 2400ms SOA). The interaction of primary interest, between group and trial type, was also significant, ($F_{(1,18)} = 8.4 \ p = 0.01$). Group IT showed a much smaller compatibility effect (9ms) than group CT (34ms). Simple effects analysis revealed that the difference in RT between compatible and incompatible trials was significant for group CT ($F_{(1,18)} = 29.7 \ p < 0.001$), but not for group IT ($F_{(1,18)} = 1.8 \ p = 0.194$). Thus the group which received compatible training showed a movement compatibility effect, while the group which received incompatible training did not.
Figure 14 – Mean RT on compatible and incompatible trials in Experiment 8. Data from both Group Compatible Training (CT) and Group Incompatible Training (IT) are displayed.Outlined columns represent compatible trials and blocked columns represent incompatible trials. Vertical bars indicate SEM.

To find out whether the magnitude of the compatibility effect varied with response speed, a bin analysis was performed on these data as in Experiment 7. Mean RT to compatible and incompatible trials for group CT and IT at each bin are presented in Figure 15. These data were analysed using ANOVA with trial type (compatible, incompatible), and bin (slow, medium, fast) as within-subjects factors, and group (CT or IT), as the between-subjects factor. The analysis revealed significant main effects of trial type ($F(1,18) = 16.2 \ p = 0.001$) and bin ($F(2,36) = 307.7 \ p < 0.001$). Significant interactions were also found between the trial type and group factors ($F(1,18) = 5.0 \ p = 0.04$), and between the trial type and bin factors ($F(2,36) = 6.1 \ p = 0.014$). However, the three-way interaction between group, trial type, and bin was not reliable ($F(2,36) < 1$). The trial type x bin interaction reflects the fact that the movement compatibility effect increased with RT. Thus, in the fastest bin, responding was only 4.4ms faster in
compatible than in incompatible trials, and in the medium bin this difference was 6ms, but in the slowest bin the difference was 17ms. Although it increased with RT, simple effects analysis revealed that the compatibility effect was significant at each bin (slow $F_{(1,18)} = 12.7 \ p = 0.002$, medium $F_{(1,18)} = 19.0 \ p < 0.001$, fast $F_{(1,18)} = 12.7 \ p = 0.002$).

Figure 15 – Mean RT on compatible and incompatible trials at fast, medium and slow response bins in Experiment 8. Data from both Group Compatible Training (CT) and Group Incompatible Training (IT) are displayed. Outlined columns represent compatible trials and blocked columns represent incompatible trials. Vertical bars indicate SEM.

Thus, performance on a task which is sensitive to movement compatibility (Experiment 7) was found in Experiment 8 to vary with the type of training received approximately 24hrs prior to testing. The difference in response speed between compatible and incompatible trials was significantly reduced for the group which had received incompatible training. In this group, RTs on compatible trials were not significantly faster than on incompatible trials. This experiment demonstrates that the
movement compatibility effect observed in Experiment 7 is susceptible to training of incompatible responses. Bin analysis revealed that the movement compatibility effect is present at every bin, but increases as RT increases, and that this effect does not vary according to the type of preceding training.

4.3 General Discussion

Using hand opening and closing movements on orthogonal dimensions of stimulus and response movements, Experiment 7 compared RT on trials in which stimulus and response movements were compatible, to trials where they were incompatible. Responding was faster on compatible trials than on incompatible trials, i.e. a movement compatibility effect was found. Experiment 8 investigated the effect of compatible and incompatible training on this movement compatibility effect. Training involved participants producing a response movement which matched (Group CT), or did not match (Group IT), the stimulus movement. The results indicated that Group IT learned more than CT during training. Test performance revealed that participants who received compatible training showed the movement compatibility effect, while participants who had received incompatible training did not.

Following previous researchers (e.g. Brass et al., 2001; Brass et al., 2000; Stürmer et al., 2000) the movement compatibility effect demonstrated in Experiment 7 is interpreted as showing that perception of an action activates the motor representation of that action. When stimulus and response movements match, execution of response is facilitated. When the two movements do not match, the incorrect matching response must be inhibited before the correct response can be performed. Neutral stimuli were
not presented to participants to establish a baseline from which deviation due to compatible and incompatible trials could be measured. Therefore the results of this experiment do not indicate whether compatible responses facilitated, or incompatible movements retarded, response speed.

The movement compatibility effect was found even though stimulus and response movements were made on orthogonal dimensions. This feature of the experimental design was intended to rule out an explanation of the movement compatibility effect based on simple spatial compatibility. However, there is some evidence that higher-order spatial compatibility effects can be found when characteristics of the response or stimulus set encourage spatial encoding in non-veridical terms (Hommel & Lippa, 1995; Lippa, 1996; Prinz, 1997). For example, Hommel and Lippa (1995) displayed stimuli that were superimposed on the eyes of a human face to which left or right hand responses were made. Spatial compatibility effects were observed even when the face was rotated by 90° such that the stimuli appeared above or below fixation. The visual context produced spatial coding of the stimuli as left and right, even though the stimuli did not actually vary on the horizontal dimension.

Two factors suggest that the compatibility effects observed in the present experiments were not due to higher-order spatial compatibility. First, unlike faces, hands do not have a canonical orientation (see Valentine, 1988 for a review) and so are not likely to be mentally rotated. Second, research on orthogonal spatial compatibility suggests that compatibility effects between horizontal stimuli and vertical responses do not occur under the conditions observed in the present experiments. Lippa (1996) compared transverse horizontal hand responses (see Figure 10, labelled as vertical in
Lippa, 1996), to horizontal stimuli (and vice versa). Orthogonal compatibility was only demonstrated in situations where hand position encouraged implicit coding of the non-veridical orthogonal dimension. In situations where stimulus and response positions were most equivalent to those used in the present experiments, orthogonal compatibility was not found (see also Michaels & Schilder, 1991, midline experiment).

While it is clear that in Experiment 8 incompatible, or counter-imitative, training resulted in the removal of the movement compatibility effect, the implications for theories of imitation are less obvious. It has been suggested by a number of researchers (Brass et al., 2001, Chapter 1; Prinz, 1997) that the movement compatibility effect is based on the same processes as imitation; that both involve a motor representation being activated upon action perception. If this is correct, then factors affecting movement compatibility can be construed as affecting the processes that normally mediate imitation. This experiment found that the movement compatibility effect is modifiable through experience. By implication, it is suggested that the imitation system is also open to modification by experience.

Experience-dependent changes to the processes which mediate imitation would be consistent with ASL and Ideomotor theories but not with AIM, which postulates that imitation is mediated by an innate cognitive module. However, it is possible that the processes which mediate imitation are unaffected in this experiment. Instead, short-term counter-imitative effects of training may compete for control of action with the processes of imitation and mask the normal movement compatibility effect. These short-term effects would speed incompatible responses while the normal processes of
imitation would speed compatible responses. The net result would be the removal of
the movement compatibility effect in the absence of any change to the normal
imitative process. Such a situation could occur whether the imitation system is innate
or experience-based.

In considering whether short-term, task-specific factors or modification of imitative
processes are responsible for these results, reference can be made to previous work on
modification of spatial compatibility effects through training (Tagliabue et al., 2000).
Tagliabue et al used connectionist modelling to investigate whether their results were
due to short-term, task-specific factors, or to a modification of existing long-term
SRC effects. They reasoned as follows: If incompatible training weakens long-term
associations responsible for SRC effects (Figure 16d), or establishes new long-term
links between incompatible stimuli and responses (Figure 16c), then the relationship
between response speed and the SRC effect should not change. Stimulus presentation
would activate long-term links which affect responding in a consistent manner as RT
changes. If long-term links usually show an increasing affect on behaviour as RT
increases, then a weakening of those links would still result in an increasing affect on
behaviour as RT increases but the magnitude of the difference between compatible
and incompatible trials would be smaller.

In contrast, if training effects are short-term (Figure 16, a and b), then the effect of
incompatible training should increase with RT and thus change the relationship
between the SRC effect and response speed. This is because short-term effects are
slower to affect behaviour than long-term effects, and so their effect would increase as
RT increases. This would be true whether short-term effects are mediated by
Figure 16 – Possible effects of counter-imitative training: (a) and (b) illustrate the formation of short-term associations on a modular imitative system (a), and on an associative-learning based imitative system (b). Illustrations (c) and (d) portray the effects of counter-imitative training on long-term imitative associations. (c) portrays the formation of new long-term counter-imitative association, while (d) illustrates a weakening of long-term imitative association. (Dashed line - short-term association, unbroken line - long-term association, oval – perceptual representation, rectangle – motor representation).
stimulus-response associations or a carry-over of task instructions. Effects are slow as stimuli have to processed for relevance to the current task before activating the relevant response (S-R association explanation), or because conscious responses made to stimuli are slower than automatic (for supporting evidence see e.g. Brass et al., 2000).

Data from Experiment 8, and from the studies of Brass, Bekkering and Prinz (2001) and from Stürmer, Aschersleben and Prinz (2000), suggest that movement compatibility effects increase with RT. If the relationship between the movement compatibility effect and RT is inputted into the model used by Tagliabue et al, then the following predictions are drawn: If incompatible training produces short-term effects then the movement compatibility effect should show a smaller increase with RT compared to the situation where incompatible training has not been given. Alternatively, if the effect of incompatible training is to weaken long-term associations, then the overall movement compatibility effect should be smaller, but increase with RT in the same manner as the group which received compatible training.

Results of Experiment 8 favour the interpretation that incompatible training affected the long-term mechanism responsible for producing the movement compatibility effect. Although the overall compatibility effect was smaller for the group which received incompatible training, the effect still increased as RT increased, and this increase was the same as shown by the group which received compatible training. This interpretation is justified according to the model of Tagliabue et al (2000), but it rests on a null effect (that the bin x group x trial type interaction is not significant).
Although this was the case in our experiment ($F_{(2,36)} < 1$) a low sample size meant that statistical power was extremely low (0.1). Therefore, this result should be viewed with caution until a further experiment with greater statistical power can be performed.

Further evidence suggesting that the results of Experiment 8 were not due to incompatible short-term associations comes from the literature on task switching. Task switching refers to situations where a task is performed with one set of stimulus-response (S-R) mappings, and then another task is performed with competing S-R mappings. It is generally observed that there is an RT cost upon transfer to the new S-R mappings (e.g. Allport, Styles, & Hsieh, 1994; Fagot, 1994). An RT cost of this kind could be responsible for the reduction in the compatibility effect seen in Experiment 8 after incompatible training. Participants in group IT first perform a task with one set of (incompatible) S-R mappings and then perform a task with opposite (compatible) S-R mappings. It is possible that the reduction in the movement compatibility effect is a result of changing S-R mappings from training to test, and does not reflect alteration of a long-term imitation system. This task-switching explanation is plausible in the light of evidence that the cost of task switching is mediated by negative priming of the previously compatible response (and thus could explain why incompatible training has a greater effect on compatible trials than incompatible trials in Experiment 8) and has been observed over 100 trials of the second task (Allport & Wylie, 2000).

However, one feature of the RT cost of task switching means it is unlikely to explain the results of Experiment 8. The task switching RT cost decays extremely rapidly over
a small number of trials (Allport & Wylie, 2000). If task switching was responsible for the effects observed in Experiment 8, different effects should be seen in block 1 (the first 72 trials), and block 2 (trials 73-144). This is because large costs of task switching should be observed in the first few trials of block 1, but these effects would decay rapidly and be small on later trials. This difference in effects over blocks would be manifested as a significant block x group x trial type interaction, and yet this interaction was not significant in Experiment 8 ($F_{(1,18)} < 1$). Again, caution is necessary in interpreting the absence of an interaction with low statistical power (0.12), but the absence of this interaction supports the conclusion drawn from the RT distribution analysis presented above.

In conclusion. The experiments reported here have made some progress in investigating whether imitation is based on an innate module, or an experience-based system. The movement compatibility effect was used as a measure of imitative strength, due to its presumed reliance on the same system that mediates imitation. Experiment 7 demonstrated a movement compatibility effect while controlling for simple spatial compatibility while Experiment 8 investigated the susceptibility of this effect to counter-imitative training. It was found that counter-imitative training reduced the movement compatibility effect but did not change its distribution over length of RT. Two competing hypotheses as to the cause of the disappearance of the movement compatibility were discussed; that incompatible training resulted in the modification of the long-term movement compatibility effect, or that short-term, task-specific effects masked the movement compatibility effect. Reference to a modified model of spatial compatibility following incompatible training originally proposed by Tagliabue et al (2000), and the literature on ‘task-switching’, favoured the former
hypothesis. The hypothesis that incompatible training modified the movement compatibility effect is consistent with the conclusion that imitation is based on experience-dependent processes, and favours the ASL or Ideomotor theories of imitation.
Chapter 5: General Discussion

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5.1 Overview

This chapter discusses the results of the experiments reported in this thesis with reference to the theories of imitation presented in Chapter 1. The three theoretical differences described in Chapter 1 and investigated in Chapters 2, 3, and 4 are separately addressed. The first of these is whether effector-dependant learning can occur through observation (Section 5.2). The second is concerned with the role of awareness in imitation (Section 5.3). The third difference relates to the role of experience in imitation (Section 5.4). Within each section; results from the present experiments are summarised (subsection 1), their implications with respect to theories of imitation are discussed (subsection 2), any limitations of the experiments are presented (subsection 3), and outstanding questions are detailed (subsection 4). Section 5.5 presents the conclusions about the mechanisms of imitation which can be made from the results of experiments reported in this thesis.

5.2 Effector-dependent Learning by Observation

5.2.1 Summary

Experiments 1 - 3 (Chapter 2) aimed to establish whether effector-dependent motor representations could be formed by observation of a movement sequence using the SRT task of Nissen and Bullemer (1987). The stimulus sequence upon which participants were trained in these experiments was six-items in length and had a unique structure. In all experiments, participants who had the opportunity to acquire sequence knowledge by observing a model’s responses were compared with control participants who had no opportunity to learn the sequence during training. Initial tests
detected any sequence knowledge. Transfer tests were designed in order to determine how any sequence knowledge had been encoded by disambiguating learning of motor responses and, stimulus (Experiments 1 and 2), or response (Experiment 3), locations.

The results of all three experiments indicate that participants who observed a model’s responses learned the sequence in an effector-dependent fashion, i.e. sequence knowledge could not be expressed with effectors other than those observed during training. In addition, the results of free generation (Experiment 1), and recognition (Experiment 2), tests suggest that participants who learned the sequence through observation were aware of what they had learned.

5.2.2 Interpretation

Experiments 1 – 3 were designed to discover whether effector-dependent representations could be formed through observation of a novel movement sequence. Results indicated that sequence knowledge gained through observation could only be expressed using the effectors which had been used by the model. Thus, observation of a novel finger-movement sequence prompted the formation of effector-dependent motor representations in the observer.

This finding is difficult to reconcile with the AIM and Ideomotor theories of imitation, but is predicted by the ASL model. The ASL model states that, under some circumstances, action observation may lead to a motor representation of the observed action being activated without intermediate representation. These observation-activated motor representations will be effector-dependent providing that the observed action has been consistently linked with a single, distinct set of muscles. The
formation of effector-dependent motor representations through observation is incompatible with the AIM and Ideomotor theories because of their assertion that action representations are subject to (AIM), or accompanied by (Ideomotor), flexible, higher-order encoding which should enable performance of an observed movement with any effector.

5.2.3 Limitations

Experiments 1 and 2 attempted to determine both the level of effector-dependence and awareness of information gained through observation of a movement sequence. Both experiments included transfer tests to discover the nature of sequence representations. Experiment 1 included a generation test and Experiment 2 included a recognition test in order to identify how aware participants were of their sequence knowledge. The results of these experiments indicated that participants’ knowledge was stored as explicit effector-dependent motor representations. Three factors, both theoretical and methodological, make the observed pattern of results unlikely.

The first is that if participants are aware of their knowledge, then one would not expect the constraint on expression of this knowledge seen with effector-dependent motor representations. Knowledge of which we are consciously aware should always be flexible and open to recoding, a line of argument which has led theorists such as Hikosaka et al (2002) to argue that effector-dependent representations must always be implicit. If this argument is accepted then one must look to methodological flaws in the experimental design which may have caused this erroneous combination of results.
Two weaknesses in the designs of Experiments 1 and 2 may have produced these results. The first relates to the combination of transfer and awareness tests in the same experiment. The order of transfer tests and the test of awareness was not counterbalanced; consequently the test of awareness was open to contamination as a result of participants having performed the transfer tests. It is quite possible that learning was initially effector-dependent and implicit, but that completion of the transfer tests caused sequence knowledge to become explicit. While the order of the transfer tests and the test of awareness should have been counterbalanced in order to provide an opportunity to identify any effects of test order, the fixed order of these tests reflected the primary aim of these experiments which was to discover the level of effector-dependence of sequence knowledge. As a result of this focus, transfer tests were always completed before the test of awareness. Experiments 4 - 6, in which the primary aim was to assess how aware participants were of their sequence knowledge, did not include transfer tests to avoid any such effect on awareness.

The second methodological flaw which may have produced the combination of effector-dependence and explicit knowledge found in experiments 1 and 2 relates to the tests of awareness. Both of the tests used in these experiments may indicate explicit knowledge when knowledge is actually implicit. Knowledge is judged to be explicit on the free generation test when participants are successfully able to generate the training sequence without being cued by stimuli. However, successful production of the sequence may be based not on explicit knowledge, but on an implicit motor program which is ‘run’ without conscious awareness of the contents of the motor program.
Explicit knowledge is demonstrated on the recognition test when participants respond faster to training than new sequences and also rate training sequence fragments as more familiar than new sequences. However, such a pattern of results is also possible when knowledge is implicit. In this case successful recognition performance could be based on a 'feeling of fluency' (Shanks and Johnstone, 1999). This would involve participants recognising that they respond faster to some (training) sequences, (which may be based on implicit motor knowledge), and rating these sequences as more familiar. This process would produce successful recognition performance without participants being aware of their sequence knowledge.

Despite these weaknesses, the generation and recognition tests are the most widely used test of awareness, especially in combination with an SRT task (Russeler, Henninghausen, Munte, & Rosler, 2003), and Shanks and St John (1994) have argued that the recognition test is the most sensitive of all current tests of awareness. These two factors caused these tests to be used in Experiments 1 and 2, and the recognition test to be used in Experiments 5 and 6, where the primary research focus was on participants' level of awareness. Indeed, the limitations of the recognition test in indicating implicit knowledge make the suggestion of implicit learning shown by observers of a model's response in Experiments 5 and 6 all the more striking.

5.2.4 Outstanding Questions

An important question which has not been answered by this thesis relates to the conditions under which effector-dependent learning can occur by observation. ASL claims that learning will be effector-dependent when motor representations which code for a distinct set of muscles are activated by perceptual information without
intermediate symbolic representation. This claim merits further investigation, perhaps by assessing the nature of information processing which occurs in instructed imitation experiments (“Do as I do”), such as that of Bekkering, Wohlschlager, and Gattis (2000). It has been demonstrated that, at least in infants, effector-dependent representations are not usually formed under these circumstances. The reasons why an instruction to imitate should affect the encoding of observed movements has not been explicitly addressed by ASL, and merits further investigation.

5.3 The Role of Awareness in Imitation

5.3.1 Summary
Experiments 4 - 6 (Chapter 3) aimed to determine whether observational sequence learning could be implicit. The SRT task was used in these experiments but, in contrast to experiments in Chapter 2, the sequence to be learned was twelve items in length and had a second-order conditional (SOC) structure. Experiment 4 compared sequence knowledge gained through observation of screen stimuli and a model’s responses, and observation of screen stimuli alone, with untrained controls. Results showed no difference between observers of screen stimuli alone and observers of screen stimuli and a model’s responses. Both groups of observers demonstrated greater sequence knowledge than untrained controls i.e. they exhibited observational sequence learning of a 12-item SOC sequence.

Experiment 5 sought to compare the magnitude of learning gained through task practice with observation of stimuli alone and observation of stimuli and a model’s responses. In addition, a recognition test was used to determine how aware
participants were of any sequence knowledge they had gained. Results implied that observational training led to sequence knowledge which was equal in magnitude to that gained through physical practice. Results of the recognition test suggested that participants were aware of sequence knowledge gained through physical practice and observation of screen stimuli alone, but were not aware of sequence information gained through observation of screen stimuli and a model’s responses.

Experiment 6 investigated whether observation of a model’s responses, but not screen stimuli, could support learning of a 12-item SOC sequence, and whether participants were aware of any sequence knowledge gained through this type of observational training. Results showed that observers of a model’s response gained more sequence knowledge than untrained controls. Additionally, results suggested that sequence knowledge gained through response observation was implicit; i.e. that participants were unaware of their sequence knowledge.

5.3.2 Interpretation
Experiments 4 - 6 investigated the level of awareness which accompanies observational learning of a movement sequence. Results implied that observation of a movement sequence could support learning of the sequence and that participants had learned implicitly. Such a characteristic of observational motor learning is incompatible with the AIM model, but is consistent with both the ASL and Ideomotor theories of imitation.

Implicit learning by imitation is inconsistent with the AIM model due to its reliance on active, effortful processing. The AIM model claims that the desired and actual
states of the imitator’s body are actively compared to produce a movement target. The desired state of the imitator’s body is obtained by inferring the model’s action goals from their movements. It is possible that such active, effortful processing may lead to learning which is implicit, particularly in situations where task characteristics mean explicit learning is unlikely to occur. However these experiments were not an example of such a task. The Practice and Observe Screen groups showed explicit knowledge of the sequence, showing that explicit learning was possible under these experimental conditions. AIM would predict that the groups most likely to develop explicit knowledge would be the Observe Screen and Hands, and Observe Hands groups, due to their active effortful processing of the movement stimuli. However, both of these groups showed some evidence of implicit knowledge when tested.

In contrast, both ASL and Ideomotor theories posit that imitation may occur without conscious representation. In both of these theories, visual action percepts may activate motor (ASL), or action (Ideomotor), representations directly, without the need for conscious effortful processing. In such situations learning by imitation will be implicit.

5.3.3 Limitations

Experiments 1 – 3 investigated whether observation of a movement sequence would enable the observer to learn the sequence, and if so, how the sequence was represented. The sequence used in these experiments was short and had a simple structure. This type of sequence was chosen for practical reasons. As the aim of the experiments was to determine whether it was possible to form effector-dependent
representations through observation, experimental parameters were guided by the only experiment in the literature to report this type of learning (Heyes and Foster, 2002).

Experiments 4 – 6 aimed to discover whether sequence knowledge gained through observation could be implicit. These experiments used a longer sequence with a more complex structure than those in Chapter 2. Again, the type of sequence used in these experiments was chosen for practical reasons. The overwhelming majority of studies reporting implicit practice-based sequence learning had used 10 or 12-item sequences with a complex structure (e.g. Exner, Koschack, & Irle, 2002; Kelly & Burton, 2001; Reber & Squire, 1998).

While the choice of sequences used in Experiments 1 - 6 maximised the chances of obtaining useful data, comparisons between the results of experiments investigating effector-dependence and those investigating awareness of sequence knowledge are problematic due to the different sequences used in the experiments. Such a comparison would have been especially beneficial in explaining the suggestion that observation of a model’s response may have produced implicit sequence knowledge. An explanation of these results was forwarded which rests on the assumption that observation of a model’s response produced implicit motor learning. Although experiments 1 - 3 suggest that motor representations can be formed through observation of a model’s responses, and experiments 4 – 6 suggest that sequence knowledge gained through observation of a model’s responses can be implicit, the differences in sequence length and structure between the two sets of experiments means that results cannot be combined. Thus, these results do not show that implicit
motor learning can occur through observation of a model's responses, although they suggest that such learning may be possible.

A full investigation of effector-dependence and awareness of sequence knowledge gained through observation would include both issues being investigated using unique and complex sequences. Unfortunately a lack of time and space prevented such an investigation being included here, but is recommended for future investigation. Such an extension of the present experiments would not only provide a more thorough and general answer to the questions of effector-dependence and awareness of observational sequence learning, but may also have important theoretical implications. Several studies have demonstrated differential effects of a number of variables on learning of complex and unique sequences. These differences include effects of; a secondary task on learning (Cohen, Ivry, & Keele, 1990 experiments 3 and 4), age on learning competence (Howard & Howard, 2001; Howard & Howard, 1997), the intention to learn (Curran & Keele, 1993), and of observation on learning (Howard, Mutter, & Howard, 1992). If sequence structure affects either the effector-dependence or awareness of sequence information gained through movement observation, then theories of imitation must be able to explain such an effect.

A feature of experiments 1 – 6 which deviates from standard practice-based SRT research is the lack of sequence counter-balancing. Many experimenters counterbalance training and new sequences to avoid confounding sequence type (training vs. new), with sequence difficulty (e.g. Schvaneveldt & Gomez, 1998). In most studies of practice-based learning an effect of sequence type on RT is looked for, learning is demonstrated by faster responses to training compared to new
sequences. Sequence counterbalancing is important for these experiments as any increase in RT from training to new sequences may be caused by differences in the ease of sequence production rather than sequence knowledge. However, the present experiments compare groups of observers with groups of control participants who have no opportunity to learn the sequence. Learning due to observation is indexed by a greater increase in RT upon transfer to the new sequence shown by observers, compared to that shown by controls. With this type of experimental design a difference in ease of production between training and new sequences would be less likely to produce spurious results as both groups of participants should be affected equally. However, differences in the ease of production of training and new sequences may affect the amount of learning shown through observation by introducing floor or ceiling effects which may mask the effects of observational learning. The generality of experiments 1 – 6 would have been increased had training and new sequences been counterbalanced and different pairs of training and new sequences been used for each experiment.

5.3.4 Outstanding Questions
An interesting question that has not been answered by the experiments in this thesis concerns the relationship between the level of effector-dependence and awareness of representations formed through action observation. Hikosaka et al (2002) have argued that effector-dependent motor representations are necessarily implicit. The results of Experiments 1 – 6 in Chapters 2 and 3 are ambivalent with respect to a relationship between these two properties. While Experiments 2 and 3 seemed to suggest that the observational sequence learning demonstrated in these experiments was explicit and effector-dependent, methodological problems cast doubt on the results of the tests of
awareness. Differences in the length and structure of sequences used in Chapters 2
and 3 mean that the results of experiments investigating effector-dependence cannot
be generalised to those testing awareness of learned information, and vice versa.
However, the results of experiments in Chapter 2 suggest effector-dependent motor
learning can occur through observation. If one accepts the arguments of Hikosaka et
al (2002), these results can explain the difference in sequence awareness between
observers of inanimate stimuli and human movement seen in Experiments 5 and 6.

Future experiments should aim to obtain valid measures of effector-dependence and
awareness of observational learning in order to investigate this question. One possible
mechanism for such testing would be to use two modified recognition tests. The tests
would follow the format of the recognition tests used in the present experiments i.e.
old and new sequences would be executed and then rated. However, in one of the
recognition tests participants would respond using the same effectors as during
training but to different stimuli, and in the other test training stimuli would be
presented to which participants respond with effectors other than those upon which
they were trained. Such tests would provide a method of testing both the level of
effector-dependence, and awareness, of participants’ sequence knowledge

5.4 The Role of Experience in Imitation

5.4.1 Summary
Experiments 7 and 8 (Chapter 4) provide an initial investigation of the susceptibility
of the movement compatibility effect to counter-imitative training. Experiment 7
established the existence of a movement compatibility effect which was
unconfounded with spatial compatibility. Hand movements were performed upon
detection of movement of a hand presented on a computer screen. The stimulus hand
either demonstrated a matching (compatible trials), or non-matching (incompatible
trials), movement. RT on compatible trials was significantly faster than on
incompatible trials.

Participants in Experiment 8 received either compatible or incompatible training
before completing the same task as those in Experiment 7. Training involved a choice
RT task in which participants responded to observed stimulus movement with either a
matching (compatible training), or a non-matching (incompatible training),
movement. On test, participants who had received compatible training did, but those
who had received incompatible training did not, exhibit the movement compatibility
effect shown in Experiment 7.

5.4.2 Interpretation
Experiments 7 and 8 investigated the role of experience in imitation. Results of these
experiments lead to the conclusion that the system responsible for imitation is
susceptible to training, and therefore experience-dependent. This issue clearly
separates the AIM model from ASL and Ideomotor theories, as the AIM model
suggests that imitation is mediated by an innate cognitive module. The finding that the
imitation system can be modified through a small amount of counter-imitative
experience is not compatible with an innate, hard-wired view of imitation. Such an
effect of training on imitation would be predicted by both the ASL and Ideomotor
theories however. These theories contend that imitative ability is developed through
learning: The ASL model argues that perceptual and motor representations of actions
become associated, while Ideomotor Theory argues that associations must be formed between actions and their effects.

5.4.3 Limitations

Experiment 8 showed that incompatible training can result in the removal of a previously observed movement compatibility effect (Experiment 7). Discussion of these results focussed on whether incompatible training had modified the normal process of imitation responsible for producing the movement compatibility effect, or had formed incompatible short-term associations which masked the normal compatibility effect. Although it was concluded that the long-term imitation system had been modified by incompatible training, this conclusion rested on the absence of two interactions. Power analysis indicated that these results had very low statistical power, and thus were unlikely to detect any significant effect present. While this indicates that a further experiment should be run which replicates Experiment 8 with greater numbers of participants, it should be noted that retrospective power analysis has been severely criticised by a number of statisticians due to its direct inverse relationship with the observed significance of an effect. Thus, if an observed alpha value approaches 0, then observed power will approach 1. Conversely, as observed alpha increases, so observed power will decrease (e.g. Lenth, 2001; Hoenig & Heisey, 2001).

An alternative approach is to compare the number of participants per group in Experiment 8 (ten) with other experiments which have demonstrated movement compatibility effects. Clearly most directly comparable is Experiment 7, which also used ten participants per group. Other experiments demonstrating movement
compatibility effects have generally used less participants than the present experiments (Brass et al, 2000, n = 8; Brass et al, 2001, n = 8; Sturmer et al, 2000, n = 8 - 10). Although these experiments did not investigate the impact of counter-imitative training on a movement compatibility effect, they do illustrate that the number of participants in Experiment 8 was consistent with related experiments reported in the literature.

5.4.4 Outstanding Questions

These results clearly favour an experience-based model of imitation which relies on learning. If imitation relies on learning then neonates should be severely limited in their capacity to imitate. As shown in Chapter 1, there is considerable debate over whether imitation has been shown in neonates, with several laboratories claiming to have demonstrated neonatal imitation (e.g. Field, Goldstein, Vaga-Lahr, & Porter, 1986; Field et al., 1983; Meltzoff & Moore, 1977, 1983, 1994), and several laboratories claiming that the evidence is flawed or inconclusive (e.g. Anisfeld 1991, 1996, 2001, in press, Couturier-Fagan 1996). The experiments reported in this thesis would suggest that neonatal imitation should be extremely limited, but only if neonatal imitation is governed by the same system as adult imitation. While it may be parsimonious to suggest that neonatal and adult imitation are the product of one system, some evidence exists which suggests that this assumption may not be correct. This includes research which has revealed that the imitative ability demonstrated by neonates and infants within the first weeks of life disappears by 3 months for normal children, and by 4 months for children with Down’s syndrome (Heimann, Ullstadius & Swerlander, 1998; Heimann, Nelson & Schaller, 1989), and that which shows that
neonatal imitative ability is unrelated to imitative ability at 1 year of age (Heimann & Ullstadius, 1999).

5.5 Conclusions

This set of results strongly favours the ASL theory of imitation, with Ideomotor Theory also being well supported. None of the results obtained in this study support the characterisation of imitation described by the AIM model. This enables us to compare the AIM model with the other theories to identify some features of the imitation system revealed by the experiments contained in this thesis. The two main differences between the ASL and Ideomotor, and AIM theories of imitation are the roles of experience and awareness. These results favour an experience-based model of imitation which is not solely reliant on conscious, effortful processing. Consequently, any model of imitation must be able to account for the adaptive nature of imitative responses, and include the capacity for automatic imitation.

The main difference between the ASL and Ideomotor theories of imitation is the structure of the representation which controls action. Ideomotor theory states that this representation contains all effects of performing the action coded on a number of levels. Thus, simple visual descriptions of the movement will be included in the representation, as will goals of the movement, and symbolic representations. In contrast, the ASL model posits that representations activated through perception contain only motor commands necessary to produce the action and proprioceptive information received when the movement is performed.
It is this difference in representation structure which prompts the differential prediction of effector-dependence through observation. If an Ideomotor representation is activated, then information will be available to guide production with any effector, due to the inclusion of higher-order cognitive representations in the action representation. However, if the motor representation described by ASL theory is activated, then this representation will be specific to one effector.

The difference between the ASL and Ideomotor theories is based on differences in action representations, not on the mechanisms of imitation which allow the correspondence problem to be solved. Both theories suggest that the correspondence problem is solved by learning of bi-directional association between representations necessary to produce imitative actions, and their effects on the environment. The ASL theory is solely concerned with perceptual representations of the action, while Ideomotor Theory suggests that representations contain action effects on a number of perceptual and cognitive levels.

In summary: This thesis has assessed three theories of imitation concerned with solving the correspondence problem: Associative Sequence Learning (Heyes and Ray, 2000), Ideomotor Theory (e.g. Prinz, 1997), and Active Intermodal Mapping (e.g. Meltzoff and Moore, 1997). These theories were evaluated based on their predictions of effector-dependent learning through movement observation, awareness of information learned through imitation, and the role of experience in imitation. Results supported the combination of an experience-based imitation system which can operate without awareness described by the Associative Sequence Learning and Ideomotor theories of imitation. Furthermore, the representational structure described by the
Associative Sequence Learning Theory was found to be more plausible than that described by Ideomotor Theory, at least in the context of imitation of novel actions.
References


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