HOW DO "INVISIBLE" STIMULI INFLUENCE ACTION? VISUOMOTOR PROCESSING IN THE ABSENCE OF CONSCIOUS AWARENESS

by

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Human Kinetics)

THE UNIVERSITY OF BRITISH COLUMBIA

July 2007

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Abstract

The goal of the current research was to examine the properties of visuomotor processing occurring in the absence of conscious awareness. Specifically, we investigated the ability of a subliminal stimulus to influence the on-line control of an action (Studies 1 and 2) and the extent to which the same subliminal stimulus could influence action when the probability of it predicting the upcoming response was manipulated (Studies 3 and 4). In order to display stimuli subliminally, stimuli were presented through the psychophysical procedure of metacontrast masking - a form of backward masking in which the visibility of a briefly displayed visual stimulus (the *prime*) is greatly reduced when it is followed by a second visual stimulus (the *mask*). Thus in the present research we were interested in how the primes would influence performance. Results revealed that (1) unconscious visuomotor processing can result in the modification of an overt response, such that a goal-directed movement is adjusted in response to a subliminal stimulus and (2) the visuomotor system can be modified in response to manipulations of the prime-mask sequence presented at an unconscious level. These results imply that subliminal stimuli are not processed in a *conditionally automatic* manner. In order to explain the ability of subliminal stimuli to influence behaviour we propose an accumulator model, in which adaptations to the state of the system arising due to task constraints are reflected at the level of response activation (i.e. at the accumulators). An "accumulator" is tuned to a specific stimulus-response mapping such that if participants are instructed to make a left or right response, two separate accumulators are established with one collecting neural evidence for stimuli mapped to the left response and the other collecting neural evidence for stimuli mapped to the right response. Both primes and masks are equally effective at driving the accumulators and a response is initiated as soon as the accumulated neural evidence for one response versus the alternative response reaches a critical threshold. The level of this threshold can be set strategically, or modified without awareness, depending on the prime-mask sequence displayed.

ii

Table of Contents

ي ا

Abstract	ii
Table of Contents	
List of Tables	
List of Figures	
Acknowledgments	
Contribution of the Author	

CHAPTER 1

THESIS	OVERVIEW	1
1.1	Eye Blindness – Hand Sight: Evidence from patient populations	1
1.2	Eye Blindness – Hand Sight: Evidence from the healthy population	4
1.2.	.1 Automatic visuomotor guidance	4
1.2.	.2 Masked priming in metacontrast masking	7
1.3	Current explanations of masked priming	9
1.4	Aims of the experiments	11
1.5	Figure	

CHAPTER 2

STUDY 1: On-line control of	pointing is modified by u	inseen visual shapes	

` 2 1	Introduction	01
2.1	Introduction	
2.2	Method	
2.2.1	1 underputies internet interne	
2.2.2	2 Apparatus	
2.2.2		
2.2.4	4 Movement Analysis	
2.2.5		
2.3	Results	
2.4	Discussion	
2.5	Bridging Summary	
2.6	Table	
2.7	Figures	
2.8	References	

CHAPTER 3

STUDY 2: Can the processing of visually-masked stimuli during rapid target-directed action	ns
be mediated by the dorsal stream?	14

3.1	Introduction	4
3.2	Method	8
	1 Participants	
	2 Stimulus Display	

3.2.3	Stimuli	
3.2.4	Motion Analysis	49
3.2.5	Procedure and Design	
3.3 Da	ata Analyses and Results	51
3.3.1	Prelude: Practice Trials	
3.3.2	Part I: Presentation of Prime-Mask Sequence before Movement Onset	52
3.3.3	Part II: Presentation of Prime-Mask Sequence at Movement Onset	
3.3.3	.1 Movement characteristics of the Responders	56
3.3.3	.2 Movement characteristics of the Non-Responders	60
3.3.4	Perceptual Awareness	61
3.4 Di	scussion	61
3.5 Bi	idging Summary	65
3.6 Ta	ıbles	61
3.5 Fi	gures	70
	eferences	

CHAPTER 4

STUDY	3: Unconscious but under control: Subliminal behaviour is sensitive to	observer
	ons	
4.1	Introduction	80
4.2	Method	
4.2.		
4.2.	2 Apparatus	
4.2.		
4.2.	4 Procedure	
4.2.		
4.3	Results	
4.4	Discussion	
4.5	Conclusion	
4.6	Bridging Summary	94
4.7	Figures	96
4.8	References	102

CHAPTER 5

STUDY 4: Pusl	hing the limits of unconscious processing: Evidence for an adapti	ve
visuomotor syst	tem	
5.1 Introd	duction	
	Overview of Experiments	
	riment 1: Baseline performance	
	Methods	
5.2.1.1	Participants	
5.2.1.2	Stimuli	
5.2.1.3	Apparatus	
5.2.1.4	Procedure	

.

5	.2.1.5 Data Analysis	110
5.2.	2 Results	111
5.2.	3 Discussion	112
5.3	Experiment 2: The influence of an intentional bias on subliminal processing	112
5.3.	1 Methods	113
5	.3.1.1 Participants	113
5	.3.1.2 Apparatus and Stimuli	
5	.3.1.4 Data Analysis	114
5.3.	2 Results	114
5.3.		
5.4	Experiment 3: The influence of an unconscious bias on subliminal processing	117
5.4.	1 Methods	117
5	.4.1.1 Participants	117
5	.4.1.2 Apparatus and Stimuli	117
5	.4.1.3 Procedure	117
5	.4.1.4 Data Analysis	
5.4.	2 Results	118
5.4.		119
5.5	Experiment 4: The influence of the relationship between conscious and	
uncon	scious events on subliminal processing	121
5.5.	1 Methods	122
5	.5.1.1 Participants	122
5	.5.1.2 Apparatus and Stimuli	122
5	.5.1.3 Procedure	
5	.5.1.4 Data Analysis	
5.5.		
5.5.		
5.6	General Discussion	125
5.7	Conclusion	129
5.8	Tables	130
5.9	Figures	134
5.10	References	138

CHAPTER 6

GENER	AL DISCUSSION	141
6.1	Perceptual identification	142
6.2	Current explanations of the masked priming phenomenon	
6.2.	1 Metacontrast masking	
6.2.	2 Masked priming	
6.3	Finding 1: Subliminal visuomotor processing can take over the co	ntrol of a goal-
directe	ed movement	
6.3	1 Accumulator model of priming	
6.3	2 Visuomotor processes engaged	
6.3	3 Additional considerations	156

6.4	Finding 2: The visuomotor system can be modified in response to	unconscious
event	S	
6.4	Accumulator model of priming	
6.4		
6.5	Final considerations	
6.5	5.1 Visuomotor signals in rapid chase	
6.5	5.2 The choice of arrows as stimuli	
6.6	Conclusion	
6.7	References	
APPEN	DIX A	
A.1	The Task	
A.2	Analyses and Results	
A.3	Conclusion	
A.4	Figures	
APPEN	DIX B	
B.1	Accumulator model of priming	
APPEN	DIX C	
C.1	The Task	
C.2	Analyses and Results	
C.3	Discussion	197
C.5	Table	
C.5	Figures	
APPEN	DIX D	
	Research Ethics Board Certificate of Approval	

List of Tables

Table 2.1.	Mean (SE) response times (ms), pointing movement times (ms) and times
	of final trajectory modifications in the goal-directed movement
Table 3.1.	Mean (SD) performance for movements in which the prime-mask
	sequence was displayed before movement onset and movements were
	completed to the correct target
Table 3.2a.	Mean (SD) performance of the Responders on trials in which the prime-
	mask sequence was displayed at movement onset and movements were
	completed to the correct target
Table 3.2b.	Mean (SD) performance of the Non-Responders on trials in which the
10010 5.20.	prime-mask sequence was displayed at movement onset and movements
	were completed to the center target
	· · · · · · · · · · · · · · · · · · ·
Table 5.1.	Total number of trials completed per prime-mask combination within each
	of the four experiments. The first word (i.e. neutral, congruent,
	incongruent) indicates the relationship of the prime with the subsequent
	mask. In Experiment 2, masks are designated as high probability mask
	(displayed on 80% of all trials) or low probability mask (displayed on 20%
	of all trials). In Experiment 3, masks are designated as congruent with
	high probability prime (pointed in the same direction as the biased prime)
	or incongruent with high probability prime (pointed in the opposite
	direction to the biased prime). In Experiment 4, the number of trials are
	provided for each experimental block ($80\% = 80\%$ of all trials congruent).

.

- Table C1. Mean RT (SE) in ms and mean percentage of errors completed (SE) per prime-mask combination for the present experiment and Experiment 4, Study 4. The first word (i.e. neutral, congruent, incongruent) indicates the relationship of the prime with the subsequent mask. Results are provided for each experimental block (80% = 80% of all trials congruent). 199

List of Figures

Figure 1.1.

- Figure 2.2. Effect of prime-mask congruency on choice response times (RT) to the mask stimulus. Results are shown for congruent and incongruent prime-mask combinations with respect to mean performance on trials in which a neutral prime was displayed. Note: a negative score indicates responses were initiated faster than when a neutral prime was displayed, whereas a

ix

- Figure 2.4.Examples of mean direct spatial trajectories (open circles) and individual
perturbed spatial trajectories (solid line) under each of the three conditions
in which a left directional mask was displayed ((A) congruent prime, (B)
neutral prime or (C) incongruent prime). The center of the eccentric target
boxes are indicated by annuli (the center target box is not visible). Note
the early trajectory deviation to the left eccentric target in the congruent
trial and the initial incorrect trajectory deviation in the incongruent trial.39
- Figure 2.5.Latencies of final trajectory reversal, at which point participants began to
move to the eccentric target cued by the directional mask, with respect to
mean performance on trials in which a neutral prime preceded the
directional mask. A negative score indicates a movement was initiated
earlier to the eccentric target than when a neutral prime was displayed,
whereas a positive score indicates the modification in trajectory occurred
at a later point in time. Error bars denote standard errors. A breakdown of
the results are provided in Table 1.40
- <u>Figure 3.1.</u> (A) Overview of visual display in the pointing task. Participants were instructed to react as quickly as possible to the onset of the target boxes

Х

xi

- Figure 3.4.
 The percentage of corrected perturbed trials in which a left or right directional mask was displayed at movement onset as a function of mean movement time achieved on corresponding direct pointing trials for each participant (S01 to S11). Note the range in participants' performance.

 73

- Figure 4.1. (A) Overview of the proposed Accumulator Model of Priming. If an incoming stimulus is in the established stimulus-response set, it will contribute neural evidence to its respective accumulator while residing in a buffer (e.g. a right arrow will contribute neural evidence to a right accumulator). Both primes and masks are equally effective at driving the accumulators. We have proposed that in a pointing task, primes contribute sufficient neural activity such that a motor activation threshold (computed as the difference in the activation levels between the two response alternatives) is achieved and a response is initiated in response to the prime. Note: the timing between the prime-mask sequence displayed on the left and the state of the system modeled as accumulators on the right

xii

does not correspond directly. Changes in the level of activation of the accumulators would be delayed with respect to stimulus onset. (B) To account for our current findings we propose that participants selectively activate the response in the direction of the biased mask, such that at the time of stimulus onset the difference in activation levels between the two response alternatives favours the more probable response. Both primes and masks are still equally effective at driving the accumulators; however, modifications in the direction of the prime are only observed on trials in which the prime is pointing in the same direction as the biased mask. On these trials activity from this prime adds to the initial activation and achieves the required threshold value. In contrast, on trials in which the prime points in the opposite direction as the biased mask, prime related activity is not capable of achieving the required threshold value before input from the mask begins to activate its associated response, as additional neural activity is required to counteract

Figure 4.2. Examples of a mean direct spatial trajectory (open circles) and individual perturbed spatial trajectories (solid line) under each of the prime-mask conditions in which a low probability mask was displayed (top row) or a high probability mask was displayed (bottom row) ((A) prime pointing in the same direction as the high probability mask, (B) neutral prime or (C) prime pointing in the opposite direction to the high probability mask). The center of the eccentric target boxes are indicated by annuli (the center target box is not visible). For this participant the right mask was displayed on the majority of trials (80%). Note that an initial incorrect trajectory modification was only observed on the incongruent trial in which a prime pointing in the same direction as the high probability mask (i.e. a right prime) was displayed.

xiii

- Figure 4.4.
 Effect of the prime-mask sequence on the time of the first trajectory modification from the center target. Error bars denote standard errors.

 101
- Figure 5.2. Choice reaction times (RT) to the mask stimuli as a function of prime congruency (congruent (denoted by a square symbol), incongruent (triangle) or neutral (diamond) with respect to the mask displayed). (A) Experiment 1: Results are shown for left and responses. (B) Experiment 2: Results are displayed according to the mask presented (high probability mask: mask displayed on 80% of all trials, low probability mask: mask displayed on 20% of all trials) (C): Experiment 3: Results are displayed according to the mask's relationship with the high probability prime (congruent: mask indicated the same response as the high probability prime vs. incongruent: mask indicated the opposite response to the high probability prime). (D) Experiment 4: Results are shown for congruent and incongruent trials as a function of the proportion of congruent primemask trials displayed within an experimental block (80% (square), 50% (diamond), or 20% (triangle)). (E) The overall priming effect (congruency score) obtained in each of the four experiments (E1 = Experiment 1, etc.). In Experiment 4, results are provided for each of the three experimental

xiv

Figure 5.3. Data from Experiment 3, on trials in which the high probability prime was displayed. Each bar represents the mean reaction time (RT) obtained on 10 consecutive congruent or incongruent prime-mask trials (primary y-axis). The solid black line indicates the difference between the two RT scores. The corresponding values are provided on the secondary y-axis. Note: (1) in order to calculate these mean RT scores, trials in which participants pressed the correct key were first separated according to prime-mask congruency (i.e. congruent or incongruent trials in which the high probability prime was displayed) within each experimental block. The first 10 trials within these categories were then averaged together, then the second 10, etc. Due to the fact that participants performed a number of errors and only 48 trials were displayed per each condition, mean RT are provided for only four groups of 10 consecutive trials within each experimental block. 137

- <u>Figure A1</u>. Temporal sequence of a typical experimental trial. Left and right arrows, as well as a neutral stimulus, served as primes. Participants were instructed to make a response based on the direction of the mask arrow (e.g. to move a stylus from a home position in the direction of the mask arrow).
- Figure A2. Average displacement in the incorrect direction before movements were modified in the direction specified by the mask. Results are shown for both left and right masks as a function of prime-mask congruency (congruent, neutral or incongruent). Errors bars denote standard error. 186

XV

xvi

Figure B4.	(A) and (B) Input (and output) in a RT task 193
<u>Figure B5.</u>	(A) and (B) Input (and output) in a pointing task in which the left response is biased
<u>Figure B6.</u>	(A) and (B) Input (and output) in a RT task in which the left response is
	biased 195
<u>Figure C1</u> .	(A) Choice reaction times (RT) on congruent and incongruent trials as a function of the proportion of congruent prime-mask trials displayed (80% (denoted by a square symbol), 50% (diamond), 20% (triangle)). (B) The overall priming effect (congruency score) obtained for each of the three experimental blocks in which the proportion of congruent prime-mask trials was varied (80%, 50%, or 20% congruent). The congruency score was calculated as the difference in mean RT between incongruent and congruent prime-mask trials. Error bars denote standard errors

Acknowledgments

Vision is the art of seeing things invisible.

~ Jonathan Swift

I would like to take this opportunity to thank a number of individuals who have made my time at UBC such a rewarding experience. First and foremost, I would like to thank my supervisors, Drs. Ian Franks and Romeo Chua. Ian, you taught me the value of a good research question and challenged me to critically evaluate my research. Romeo, you showed me how to bring research to life and have passed on your enthusiasm for discovering the unknown. I eagerly await future collaborations.

In addition to my supervisors, I have had the privilege of drawing on the expertise of Dr. James Enns (committee member), Dr. J. Timothy Inglis (committee member) and Dr. David Sanderson (comprehensive exam committee member). Thank you for your probing questions and insight, which have allowed me to extend my research questions and examine my findings from a number of different perspectives.

As well, thank you to my fellow graduate students, who, in addition to taking a keen interest in my work, have become my good friends. Thank you Kirstin, Natalie, Pierre-Michel and Tony, for your continued support and encouragement. And last (but definitely not least), thank you Brendan and Mel. You two have been my family away from home - I will miss you.

Contribution of the Author

This thesis contains four experiments that have been carried out by the candidate, Erin K. Cressman, under the supervision of Dr. R. Chua (Professor, School of Human Kinetics) and Dr. I.M. Franks (Professor, School of Human Kinetics). The collection, analysis and documentation of each experiment were primarily the work of the candidate.

The above statement was written by Erin K. Cressman and agreed upon by the undersigned.

Romeo Chua, Ph.D. (graduate supervisor)

CHAPTER 1 THESIS OVERVIEW

Over 300 years ago, Leibniz proposed that unconscious perceptual processes may influence motor behaviour.

There are hundreds of pointers to the conclusion that at every moment there is any infinity of perceptions that we aren't aware of and don't reflect on For the choice that we make arises from these insensible stimuli. They mingle with the effects of outer objects and events in our bodily interiors, making us find one direction of movement more comfortable than the other. Leibniz, New Essays on Human Understanding (1704/1981)

Fast forward to the present and we find a vast amount of support for Leibniz's message. Actions can be guided by events that are never consciously perceived, as demonstrated by the host of research discussed in this chapter. However, while previous research clearly illustrates that unconscious processes can influence action, the degree to which unconscious events can impact performance is unclear. The goal of the current research is to examine the properties of visuomotor processing occurring in the absence of conscious awareness. Furthermore, by exploring the ability of subliminal visual information to contribute to motor behaviour, I will propose two possible mechanisms to explain how information is processed for action in the absence of conscious awareness.

1.1 Eye Blindness – Hand Sight: Evidence from patient populations

Individuals suffering from the neurological conditions of blindsight, visual agnosia and visual extinction readily exhibit visually guided behaviour in the absence of conscious awareness. For example, individuals diagnosed as clinically blind due to damage of the primary visual cortex (V1) have been shown to orient their eyes and arm towards the location of a visual stimulus, without any awareness of the stimulus being presented in the first place (Poppel et al., 1973; Weiskrantz, 1974; Stoerig & Cowey, 1997; Danckert & Goodale, 2000). Danckert and colleagues (2003) refer to these individuals as exhibiting action-blindsight.

In addition to object localization, Danckert and colleagues (2003) have demonstrated that movements to objects presented in the blind field of action-blindsight patients suffering from damage to selective areas of V1 (e.g. patients with cortical hemianopia) are similar in nature to movements made to objects presented in their sighted field. In the study by Danckert et al. (2003), two individuals with cortical hemianopia pointed to targets at various distances and directions from a home position. Thus, on any given trial the target was presented either in a participant's sighted field and available for conscious report or was displayed in a participant's blind field and unavailable to the conscious system. Despite insisting that they were unaware of the target when it was presented in their blind field, Danckert's patients reliably pointed to the target position. Furthermore, kinematic profiles of pointing movements completed to targets in the blind field mirrored the profiles observed when participants pointed to sighted targets (e.g. pointing movements scaled to target location, such that increases in peak velocity and time to peak velocity were observed when the target was located at a greater distance from the home position, regardless of its location in space).

In accordance with the findings of Danckert et al. (2003), Perenin and Rossetti (1996) have reported that individuals with damage to V1 can correctly orient their hand and size their finger grip appropriately when reaching out to grasp unseen visual objects. The work of Perenin and Rossetti (1996), together with the observations of Danckert et al. (2003), suggest that visual stimuli can be localized without conscious awareness and, moreover, the processes available for guiding actions towards these objects are similar to visuomotor processes engaged when stimuli are available for conscious report.

Similar conclusions can be drawn from observing the motor behaviour of patient D.F. D.F. suffers from visual agnosia, as a result of irreversible brain damage to the inferior temporal cortex (ITC). However, despite her deficiency in *seeing* orientation and form, as demonstrated by the inability to correctly (i) choose which of four line orientations depicted on a card matches the orientation of a large slot, (ii) turn a hand-held card until its orientation matches that of a slot, or (iii) indicate verbally the orientation of an oblong block placed on the table in front of her, D.F. is able to reach out and orient a hand-held card in order to post it through a slotted disc (Goodale et al., 1991). In addition, D.F. has shown accurate hand and finger movements to objects that she consciously fails to perceive in terms of shape,

orientation and size (Carey et al., 1996). Thus, D.F.'s performance on various motor and perceptual tasks further illustrates that a conscious percept is not necessary to guide action.

As a final example to illustrate that a lack of awareness does not prevent visual information from guiding motor behaviour, we can look to the neurological condition of visual extinction. Visual extinction typically arises after unilateral brain damage to the right parietal cortex (Heilman et al., 1993; Driver et al., 1997). As a result of this cortical damage, patients who suffer from visual extinction frequently fail to report brief stimuli presented in their contralesional (left) hemifield if the ipsilateral field is stimulated simultaneously (Bender, 1952). However, despite shifts in conscious awareness arising as a result of modifications to the visual display, Schenk and colleagues (2005) recently demonstrated that patients suffering from visual extinction can still use visual feedback to guide their limb in the absence of awareness. In the study by Schenk et al. (2005), a patient (V.E.) with leftsided visual extinction due to right parietal damage was asked to point towards a target with his left hand. The start position for the hand was 20 cm to the left of V.E.'s midline. Target positions were illuminated by light emitting diodes (LED) and were presented either 5 cm to the left or right of the participant's midline. A second LED was attached to the tip of V.E.'s finger. At the start of each trial, a single target LED was presented for one second. After one second the target-LED was turned off and a go tone sounded instructing V.E. to move to the target position. At the start of movement, either the target-LED was turned back on (targetonly trials), the hand LED was turned on (hand-only trials), or both the target and hand-LED were turned on (target + hand trials). After completing the pointing movement, V.E. was asked to report if he had seen the target-LED, the hand-LED or both. V.E. accurately reported the presence of the target and hand-LED on trials in which they were presented individually. However, when both LEDs were presented simultaneously, V.E. failed to report the presence of the hand-LED, which was to the left of his body-midline, on the majority of trials. Despite this lack of awareness, results indicated that performance was significantly better when visual feedback of the hand was available. Furthermore, the benefit of visual feedback on performance was of the same magnitude, regardless of whether or not it was available for conscious report.

Based on this body of work examining residual motor abilities in patients suffering from numerous neurological disorders, it is apparent that actions can be guided by visual

events in the absence of conscious awareness. Moreover, the visuomotor processes engaged by visual information unavailable to the conscious system appear to be similar to those activated when a stimulus is available for conscious report.

1.2 Eye Blindness – Hand Sight: Evidence from the healthy population

The case studies discussed above clearly demonstrate the ability of unconscious events to influence motor performance after there has been damage to certain areas of the cortex. However, as informative as these reports are, they do not allow one to make assumptions regarding unconscious visuomotor processes occurring in the general, healthy population. Furthermore, the paradigms employed with patient populations have primarily focused on how participants interact with objects presented in the environment, limiting the ability of subliminal visuomotor processes to influence performance. Thus it is unclear to what extent unconscious events can guide responses in a healthy population, in which the system has not been modified as a result of cortical damage.

There have been two general approaches to the investigation of subliminal visuomotor guidance in the healthy population. These approaches differ drastically. For example, one approach explores the degree to which motor output diverges from participants' intentions (see section 1.2.1: Automatic visuomotor guidance). The other focuses on the ability of a brief visual stimulus presented below the threshold of conscious awareness to influence reaction time to a visible stimulus presented later in time (see section 1.2.2: Masked priming in metacontrast masking). Despite their differences, both approaches make inferences about subliminal processing by examining responses to visible stimuli (i.e. stimuli available to the conscious system). The results from these two areas of research make apparent that even in the healthy population, actions can be influenced by visuomotor transformations occurring in the absence of awareness. Furthermore, results obtained in metacontrast masking paradigms suggest that subliminal processes can influence action to a greater extent than has been suggested by previous studies involving patient populations.

1.2.1 Automatic visuomotor guidance

Visuomotor transformations occurring in the absence of conscious awareness have been inferred from (1) the impact of an irrelevant stimulus property on response selection and (2) adjustments in limb trajectory in response to changes in the environment. Thus, when taken together, the results from these different tasks provide insight into how unconscious visuomotor processes influence movement initiation and the control of an ongoing movement. In general, the influence of an irrelevant stimulus property on response selection has been explored in reaction time (RT) tasks in which participants are given a specific stimulus-response mapping (i.e. participants are instructed to press either a left or right key as fast as possible depending on the identity of the presented stimulus). Surprisingly, RT to the stimulus has been shown to be influenced by its relative position (the *Simon effect*, first reported by Simon and Rudell, 1967) and intrinsic features (Tucker and Ellis, 1998; Ellis and Tucker, 2000), even when these properties are irrelevant to the task at hand.

As an example of a choice RT task demonstrating the Simon effect, De Jong and colleagues (1994) instructed participants to make a speeded response based on stimulus colour. For example, participants were instructed to press a left key when a blue square was presented and a right key when a red square was presented, irrespective of the location of the stimulus (i.e. regardless of whether the stimulus was presented to the left or right of a central fixation). De Jong and colleagues (1994) found that RT was fastest on trials in which the stimulus was presented on the same side as the required response (e.g. RT was faster on trials in which the blue square was presented to the left of fixation compared to trials in which the blue square was presented to the task, it is processed to an extent that enables it to exert a marked influence on responses to relevant stimulus features.

In addition to stimulus location, Tucker and Ellis (1998; Ellis and Tucker, 2000) have recently demonstrated that properties within an object can influence motor behaviour. In their task participants were instructed to make a key press response based on the orientation of an object (e.g. to press a left key if a cup was upright and a right key if the cup was inverted). Tucker and Ellis (1998; Ellis and Tucker, 2000) found that responses were influenced by the location of the object's handle, even though the handle did not predict the object's orientation. From these RT results and results demonstrating the *Simon Effect* (see De Jong et al., 1994), it is evident that properties of a stimulus, which need not be attended to in order to select the appropriate response, are processed, and processed to an extent that they influence action. The influence of the corresponding visuomotor transformations on RT

depends on whether or not the response activated by the irrelevant stimulus feature corresponds to the action to be completed. For example, RT is faster when the response activated by the irrelevant stimulus feature and the response activated by the identity of the stimulus correspond. The inability of participants to disregard these irrelevant features, even when they hinder performance, has led some researchers to conclude that irrelevant visual features activate a response automatically (see De Jong et al., 1994). Furthermore, in accordance with the definition of automatic (see Posner and Snyder, 1975; Shiffrin and Schneider, 1977; Bargh, 1992), these visuomotor transformations are regarded as involuntary, unintentional, autonomous and occurring outside of conscious awareness.

More direct examples of automatic visuomotor guidance, occurring in the absence of conscious awareness, can be observed during reaching movements, when the limb is in flight. For example, rapid on-line adjustments of the limb during pointing, reaching and grasping movements have been demonstrated in response to changes in the location, orientation or shape of a target object (e.g., Prablanc et al. 1986; Paulignan et al. 1991; Desmurget and Prablanc 1997; Bard et al. 1999; Desmurget et al. 1999; Pisella et al. 2000; Brenner and Smeets 2003). These limb modifications occur well in advance of the point in time at which individuals become consciously aware of the changing task environment (Castiello and Jeannerod 1991; Castiello et al. 1991; Johnson et al. 2002) and under some conditions, participants are also unaware of their own limb modifications in response to these changes (Goodale et al. 1986; Pelisson et al, 1986; Day and Lyon 2000; Fecteau et al. 2001; Chua and Enns 2005).

Moreover, on-line modifications to visually guided actions have been shown to take place regardless of one's intentions (see Day and Lyon, 2000; Pisella et al., 2000; Cressman et al., 2006a). In the study by Pisella and colleagues (2000), participants were required to point rapidly to targets that would occasionally jump to another location immediately upon the start of the movement. Participants performed under one of two instructional sets: ''location-go'' (LG) and ''location stop'' (LS). The LG instructions were to respond to the target jump by pointing to the new location, whereas LS instructions were to interrupt the movement if a target jump was detected. The main finding was that participants modified their pointing and touched down at the new target location on a significant number of trials,

regardless of instructions. From these results, Pisella and colleagues (2000) concluded that the limb is driven by an "automatic pilot", which can escape intentional control.

Taken together the results obtained from RT tasks and on-line pointing paradigms in healthy individuals demonstrate that one's limb is not under volitional control at all times. Based on this observation, researchers have concluded that even in healthy individuals, visuomotor processes do not always lead to or require conscious awareness. Furthermore, because these visuomotor processes arise in response to a stimulus, regardless of intention, researchers have typically characterized these visuomotor transformations as automatic. For example, stimulus onset or a change in stimulus position automatically activates visuomotor transformations, before conscious awareness of transpiring visual events emerges and the control of the movement can be governed according to one's intentions (see Day and Lyon 2000; Pisella et al., 2000; Cressman et al., 2006a). Finally, the corresponding visuomotor transformations appear to be completed with the purpose of allowing one to act directly on the object of interest (e.g. point to the target), in a similar manner as observed in patient populations.

1.2.2 Masked priming in metacontrast masking

As an alternative approach to the investigation of subliminal visuomotor processing in the healthy population, researchers have explored the ability of stimuli presented below the threshold of conscious awareness to influence response selection. In order to present stimuli subliminally, researchers have employed the psychophysical procedure of metacontrast masking. In general, masking refers to the reduction in visibility of a briefly displayed visual stimulus (*the prime*) when it is preceded, combined with or followed by a second stimulus (*the mask*) (for reviews see: Kahneman, 1968; Breitmeyer, 1984; Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000). Metacontrast masking is a form of backward masking, in which the visibility of the prime is reduced by a temporally lagging mask, whose shape closely fits the outer contour of the prime without overlapping it (see Figure 1a). By varying the amount of time that passes between the onset of the prime and the mask, the prime can be rendered invisible to the system responsible for conscious reports and discrimination; prime visibility is typically lowest when the interval is between 40-80 ms (Breitmeyer, 1984).

Although the primes cannot be perceived by the conscious system as a result of metacontrast masking, researchers have demonstrated that the primes influence motor responses to the mask stimuli (i.e. masked priming: the metacontrast dissociation). Specifically, both simple and choice reaction times to the mask have been shown to be faster when the mask is preceded by a prime that shares response relevant features (Fehrer and Raab, 1962; Taylor and McCloskey, 1990, 1996). As an example demonstrating this metacontrast masking dissociation, Vorberg and colleagues (2003) had participants respond as fast as possible to the left or right direction of a centrally presented large arrow by pressing a corresponding key with the left or right index finger, respectively. The large arrow masked the presence of a preceding smaller prime arrow that pointed in the same direction (congruent) or opposite direction (incongruent) as the mask. Reaction times to the large arrow were significantly faster when it was preceded by a congruent prime in comparison to an incongruent prime, even though the primes could not be consciously discriminated (see Figure 1b). In addition to orientation, reaction time benefits for congruent prime-mask sequences in comparison to incongruent prime-mask sequences have been observed when the prime and mask share the same location (Ansorge et al., 2002), shape (Neumann and Klotz, 1994), colour (Schmidt, 2002; Breitmeyer et al., 2004) or semantics (Dehaene et al., 1998; Kunde et al., 2003).

The findings obtained in metacontrast masking RT paradigms provide further support for the claim of subliminal visuomotor guidance. However, in contrast to previous findings, results obtained in metacontrast masking RT tasks demonstrate that unconscious events are not confined to influencing actions *automatically*, as a result of stimulus onset. In metacontrast masking RT paradigms, a stimulus presented below the threshold of conscious awareness influences motor responses in accordance with its identity. Specifically, a prime will influence performance if it shares a response relevant feature with the mask stimulus (e.g. the primes and masks are both arrows) (see Ansorge et al., 2002; Enns and Oriet, 2007). In order to achieve these results, the unconscious system must be capable of *identifying* the stimulus (on some level). Consequently, the results obtained from metacontrast masking RT paradigms demonstrate that subliminal visuomotor processing extends beyond the automatic localization of objects for action control. This raises the question: To what extent can unconscious processes contribute to motor behaviour?

The proposed research attempts to address this issue. In order to examine subliminal visuomotor guidance the stimuli will be presented using a metacontrast masking procedure, as this type of paradigm allows us to examine properties of subliminal processing which extend beyond object localization for action control. In addition, in contrast to previous paradigms examining unconscious processing, metacontrast masking ensures that stimuli are presented below the threshold of conscious awareness and prevents participants from gaining access to information conveyed by the prime stimuli. Thus, any influence of the primes on performance can be regarded as arising as a result of subliminal processing. Before outlining my specific research questions, I will briefly review current theories put forth to explain the metacontrast dissociation.

1.3 Current explanations of masked priming

At present, no single theory adequately explains how a prime is masked from awareness and yet is able to influence motor output in accordance with its identity. However, a number of theories have been put forth to explain different aspects of the metacontrast dissociation. Specifically, Di Lollo and colleagues (2000; see also Enns and Di Lollo; 2000) have suggested that primes are masked from conscious awareness because of cortical re-entrant processes, and Neumann (1990) and Kunde and colleagues (2003) have both adopted a top-down contingency (TDC) framework in order to explain the ability of subliminal primes to influence motor output. It is important to note that even though these theories attempt to explain different aspects of the metacontrast masking dissociation, they do not contradict each other. For example, while the cortical re-entrant processing explanation of metacontrast masking does not account for how subliminal stimuli influence action, it does not exclude prime-related activity from influencing motor responses in accordance with the TDC framework, and vice versa.

The proposal of Di Lollo and colleagues (Di Lollo et al., 2000; Enns and Di Lollo, 2000) is founded on the principle that feedback, or re-entrant, processes between brain areas (i.e. the relaying of information from higher to lower visual cortical areas) are required before conscious awareness of the stimulus can arise (Sillito et al., 1994; Hupe et al., 1998; Lamme and Roelfsema, 2000). Specifically, in the model of masking put forth by Di Lollo and colleagues, the emergence of conscious awareness is based on the activity of modules

arranged over the visual field. Each module is a circuit with connections to primary visual cortex (area V1) and a topographically related region in the extrastriate visual area. In order for conscious awareness to arise a match must occur between a descending code, representing a perceptual hypothesis, and the on-going pattern of low-level activity in V1. In a metacontrast masking RT paradigm the contents of area V1 change with the onset of the mask stimulus. Thus, Di Lollo and colleagues (Di Lollo et al., 2000; Enns and Di Lollo, 2000) propose that the prime fails to reach conscious awareness because there is a mismatch between the re-entrant prime signal and ongoing activity at the lower level.

In keeping with Di Lollo and colleagues' (Di Lollo et al., 2000, Enns and Di Lollo, 2000) explanation of metacontrast masking, Ro and colleagues (2003) have demonstrated that feedback processes in early visual cortex play a pivotal role in visual awareness. Ro et al. (2003) utilized a metacontrast masking paradigm and examined the ability of participants to detect the presence of a prime, while applying transcranial magnetic stimulation (TMS) to V1 at certain times after mask onset. As expected, the application of TMS resulted in suppression of the mask from conscious awareness. More importantly however, TMS also induced recovery of the otherwise imperceptible prime stimulus, revealing the importance of feedback processes in conscious awareness.

Based on the ability of subliminal prime stimuli to influence motor responses it is apparent that similar feedback connections are not required in order for the unconscious system to process a stimulus for action. In accordance with this suggestion, a number of theories have been put forth to explain the ability of subliminal primes to influence motor behaviour (e.g. Neumann's (1990) theory of Direct Parameter Specification and Kunde and colleagues' (2003) Action-Trigger Hypothesis). In general, these theories can be described as adopting a top-down contingency (TDC) framework of subliminal processing. The TDC framework proposes that the ability of a subliminal stimulus to influence action is dependent on what one intends to respond to, or one's pre-stimulus intentions. In particular, Neumann (1990) and Kunde et al. (2003) hypothesize that a fixed stimulus-response mapping is established based on the instructions provided. This creates appropriate release conditions or "action-triggers" for task-defined response alternatives (e.g. participants prepare to press a left key when a left arrow is presented and a right key when a right arrow is displayed). At the start of each trial, the action-triggers are activated and waiting for the last visual

parameter that will uniquely specify the required response (e.g. which hand). If an external event matches one of these conditions, the corresponding response is activated without requiring conscious mediation. Thus, the processing of subliminal information is governed by one's intentions (i.e. the established action-triggers).

Furthermore, it has been suggested that unconscious processing of stimuli within the established action-trigger set has an automatic influence on performance (Neumann, 1990; Ansorge et al., 2002; Kunde et al., 2003). For example, if the prime matches a pre-stimulus action-trigger it will have a set impact on motor performance (i.e. evoke a specific response in an immediate fashion). This proposed impact of subliminal information on action has been referred to as *conditionally automatic* (Bargh, 1992). It differs from the automatic, unconscious behaviour described in previous sections (e.g. 1.1: Evidence from patient populations and 1.2.1: Automatic visuomotor guidance), in that participants must intend to respond to a particular property of the stimulus in order for it to exert an influence. However, similar to these previous findings, the current TDC framework places restrictions on subliminal visuomotor processing. Specifically, it posits that unconscious processes, engaged during a metacontrast masking RT paradigm, are restricted to a task-relevant subliminal prime activating a corresponding action trigger.

1.4 Aims of the experiments

According to the top-down contingency framework of subliminal processing, unconscious events influence action in a *conditionally automatic* manner. While the results obtained to date in the majority of metacontrast masking paradigms clearly support this claim, there has been no systematic investigation examining the ability of subliminal processes to influence stages of movement production other than response initiation (e.g. movement execution), or possible changes in motor performance when the prime-mask sequence displayed is manipulated. Thus, the present research sought to determine the extent to which unconscious processes can influence action by examining motor performance under various task constraints. In all four studies our stimuli were presented in a metacontrast masking paradigm and findings are discussed in light of the assumptions put forth by the topdown contingency framework of subliminal processing. The first two studies examined the ability of prime stimuli to influence the on-line control of action. Having established that

subliminal stimuli can take over the control of an on-going action in an automatic manner, we next investigated modifications in unconscious visuomotor processing when the primemask sequence displayed was manipulated (Studies 3 and 4). Each study is briefly outlined below:

Study 1: On-line control of pointing is modified by unseen visual shapes

Shapes that are rendered invisible through metacontrast masking are still able to influence motor responses: a phenomenon referred to as masked priming. This has been repeatedly demonstrated in metacontrast masking reaction time paradigms, in which response time to the mask has been shown to be influenced by the preceding subliminal prime stimulus. Based on these results it is unclear whether this influence is on the control of ongoing action, or whether it merely influences the initiation of an already-programmed action. In order to address this issue we modified a masked priming procedure such that the critical prime-mask sequence was displayed during the execution of an already-initiated goaldirected pointing movement. We were interested in determining if subliminal processes could influence the on-line control of action, specifically whether subliminal stimuli could take over the control of an action after a different action had already been initiated.

Study 2: Can the processing of visually-masked stimuli during rapid target-directed actions be mediated by the dorsal stream?

The results of Study 1 indicate that stimuli presented below the threshold of conscious awareness can take over the control of a goal-directed movement. In the current study, we examined if movement adjustments observed in response to prime stimuli are automatic (i.e. arise as a result of operations occurring in the dorsal visual stream). While, previous research has proposed that unconscious visuomotor processing of masked primes could be a signature of the operation of the dorsal visual stream (see Eimer and Schlaghecken, 1998; Jaskowski et al., 2003; Schmidt, 2002), tasks investigating masked-priming have not typically been designed to be conducive to dorsal stream processing. Thus, in the present study, we examined the influence of prime stimuli on rapid visually-guided actions whose characteristics were particularly suited for dorsal stream control.

Study 3: Unconscious but under control: Subliminal behaviour is sensitive to observer expectations

The results of Study 1 and Study 2 indicate that stimuli presented below the threshold of conscious awareness can automatically take over the control of a goal-directed movement. These results differ from findings obtained in previous metacontrast masking RT paradigms. Specifically, while reaction time paradigms have consistently demonstrated that primerelated activity can influence response selection processes, subliminal processing does not typically result in an overt motor response. The difference in response patterns between the two tasks (i.e. reaction time vs. pointing task), suggests that the impact of subliminal stimuli on action is dependent on task constraints. Hence, unconscious visuomotor processes do not influence action in the automatic manner proposed by the top-down contingent framework of subliminal processing (i.e. subliminal processing does not have a set impact on motor performance). In this study we examined if the impact of the directional primes on the control of a goal-directed movement would be influenced by the baseline probability of movement in a certain direction. Participants completed the same goal-directed pointing movement as in Studies 1 and 2. However, in contrast to previous work, participants were instructed that on the majority of perturbation trials, they would be required to complete their movement in a particular direction.

Study 4: Pushing the limits of unconscious processing: Evidence for an adaptive visuomotor system

Results from the previous studies indicate that subliminal information is not processed in the *conditionally automatic* manner put forth by the current top-down contingency framework. The influence of subliminal stimuli on performance depends on the task (i.e. response selection vs. on-line control) and the ability of the stimulus to accurately predict the upcoming response. Thus, task constraints can change how the system will respond to information conveyed by a subliminal stimulus. In previous experiments we have assumed that conscious awareness of the task at hand resulted in modifications in the visuomotor system, and hence the impact of the subliminal primes on performance. In the fourth and final study we examined if the influence of subliminal processing on performance could be modulated when the task constraints were manipulated unconsciously. Specifically,

we conducted 4 separate metacontrast masking RT experiments in which the prime-mask sequence was manipulated at a conscious and unconscious level. The first experiment was conducted in order to establish participants' baseline performance. This performance was then compared to experiments in which (1) one particular mask, and hence the associated response was more probable, (2) one directional prime was more probable and (3) the proportion of congruent prime-mask trials was manipulated.

1.5 Figure

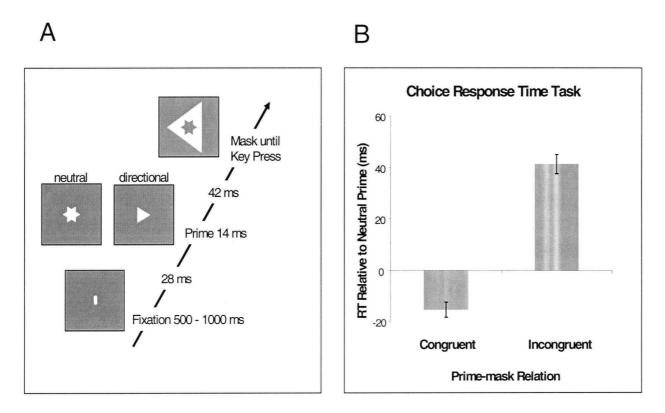


Figure 1.1. Adapted from Cressman et al. (2006b). (A) An example of the temporal sequence and stimuli displayed in a metacontrast masking reaction time (RT) task. Note: only one of the primes (the neutral or directional) would be displayed on each trial. (B) Typical effect of prime-mask congruency on choice reaction times (RT) to the mask stimulus in a metacontrast masking RT paradigm. Results are shown for congruent and incongruent prime-mask combinations with respect to mean performance on trials in which a neutral prime was displayed. Note that a negative score indicates responses were initiated faster than when a neutral prime was displayed, whereas a positive score indicates performance was slower.

1.6 References

- Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-545.
- Bard, C., Turell, Y., Fleury, M., Teasdale, N., Lamarre, Y., & Martin, O. (1999).
 Deafferentation and pointing with visual double step perturbations. *Experimental Brain Research*, 125, 410-416.
- Bargh, J.A. The ecology of automaticity: Toward establishing conditions needed to produce automatic processing effects. *The American Journal of Psychology*, 105, 181-199.
- Bender, M.B. (1952). Disorders in perception. Springfield, IL: Charles C. Thomas.
- Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.
- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1595.
- Breitmeyer, B.B., Ro, T., & Singhal, N.S. (2004). Unconscious color priming occurs at stimulus- not percept- dependent levels of processing. *Psychological Science*, 15, 198-202.
- Brenner, E., & Smeets, J.B. (2003). Perceptual requirements for fast manual responses. *Experimental Brain Research*, 153, 246-252.
- Carey, D.P., Harvey, M., & Milner, A.D. (1996). Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. Neuropsychologia, 34, 329-337.
- Castiello, U., Jeannerod, M. (1991). Measuring time to awareness. *Neuroreport*, 2, 797-800
- Castiello, U., Paulignanm Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. A study in normal subjects. *Brain*, 114, 2639-2655.
- Chua, R., & Enns, J.T. (2005). What the hand can't tell the eye: illusion of space constancy during accurate pointing. *Experimental Brain Research*, 162, 109-114
- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006a). No automatic pilot for visually guided aiming based on colour. *Experimental Brain Research*, 171, 174-183.

- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006b). On-line control of pointing is modified by unseen visual shapes. *Consciousness and Cognition*, in press.
- Danckert, J., & Goodale, M.A. (2000). Blindsight: A conscious route to unconscious vision. *Current Biology*, 10, R64-67.
- Danckert, J., Revol, P., Pisella, L., Krolak-Salmon, P., Vighetto, A., Goodale, M.A., & Rossetti, Y. (2003). Measuring unconscious actions in action-blindsight: Exploring the kinematics of pointing movements to targets in the blind field of two patients with cortical hemianopia. *Neuropsychologia*, 41, 1068-1081.
- Day, B.L., & Lyon, I.N. (2002). Voluntary modification of automatic arm movements evoked by motion of a visual target. *Experimental Brian Research*, 130, 159-168.
- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P.-F., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597-600.
- De Jong, R, Liang, C.-C., & Lauber, E. Conditional and unconditional automaticity: A dualprocess model of effects of spatial stimulus-response correspondence. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 731-750.
- Di Lollo, V., Enns, J.T., & Rensink, R.A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, 129, 481-507.
- Desmurget, M., & Prablanc, C. (1997). Postural control of three-dimensional prehension movements. *Journal of Neurophysiology*, 77, 452-464.
- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E. & Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2, 563-567.
- Driver, J., Mattingley, J.B., Rorden, C., & Davis, G. (1997). Extinction as a paradigm measure of attentional bias and restricted capacity following brain injury. In H.-O. Karnath, & P. Their (Eds.), Parietal lobe contributions to orientation in 3D space (pp. 401-429). Berlin: Springer.
- Ellis, R., & Tucker, M. (2000). Micro-affordance: the potentiation of components of action by seen objects. *British Journal of Psychology*, 9, 451-471.

- Enns, J.T., & DiLollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Enns, J.T., & Oriet, C. (2007). Visual similarity in masking and priming: The critical role of task relevance. *Advances in Cognitive Psychology*, in press.
- Fecteau, J.F., Chua, R., Franks, I.M., & Enns, J.T. (2001). Visual awareness and the on-line modification of action. *Canadian Journal of Experimental Psychology*, 55, 104-110.
- Fehrer, E., & Raab, D. (1962). Reaction time to stimuli masked by metacontrast. *Journal of Experimental Psychology*, 63, 143-147.
- Goodale, M.A., Milner, A.D., Jakobson, L.S., & Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. Nature, 349, 154-156.
- Goodale, M.A., Pelisson, D., Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, 320, 748–750.
- Heilman, K.M., Bowers, D., Valenstein, E., & Watson, R.T. (1993). Disorders of visual attention. *Bailliere's Clinical Neurology*, 2, 389-413.
- Hupe, J.M., James, A.C., Payne, B.R., Lomber, S.G., Girard, P., Bullier, J. (1998). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature*, 394, 784-787.
- Johnson, H., Van Beers, R.J., & Haggard, P. (2002). Action and awareness in pointing tasks. *Experimental Brain Research*, 146, 451-459
- Kahneman, D. (1968). Methods, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70, 404-425.
- Kunde, W., Kiesel., A., & Hoffmann, J. (2003) Conscious control over the content of unconscious cognition. *Cognition*, 10, 198-205.
- Lamme, V.A.F., & Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23, 571-579.
- Leibniz, G.W. (1981). New Essays on Human Understanding (P. Remnant & J. Bennett, Trans. & Eds.). Cambridge, England: Cambridge University Press. (Original works written ca. 1704).
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-215.

- Neumann, O., & Klotz, W. (1994). Motor responses to nonreportable, masked stimuli: Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements 1. The effects of changing object position. *Experimental Brain Research*, 83, 502-512.
- Pélisson, D., Prablanc, C., Goodale, M.A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb II: Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research*, 62, 303-311.
- Perenin, M-T., & Rossetti, Y. (1996). Grasping without form discrimination in a hemianopic field. *Neuroreport*, 7, 793-797.
- Pisella, L., Gréa, H., Tilikete, C, Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729-736.
- Poppel, E., Held, R., & Frost, D. (1973). Residual visual function after brain wounds involving the centrla visual pathway in man. *Nature*, 243, 295-296.
- Posner, M.I., & Snyder, C.R.R. (1975). Attention and cognitive control. In R.L. Solso (Ed.), Information processing and cognition: The Loyola Symposium (pp. 55-85).Hillside, NJ: Erlbaum.
- Prablanc, C., Pélisson, D., & Goodale, M.A. (1986). Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research*, 62, 293-302.
- Ro, T., Breitmeyer, B., Burton, P., Singhal, N., & Lane, D. (2003). Feedback contributions to visual awareness in human occipital cortex. *Current Biology*, 13, 1038-1041.
- Schenk, T., Schindler, I., McIntosh, R.D., & Milner, D.A. (2005). The use of visual feedback is independent of visual awareness: Evidence from visual extinction. *Experimental Brain Research*, 167, 95-102.

- Schmidt, T. (2002). The finger in flight: Real-time motor control by visually masked color stimuli. *Psychological Science*, 13, 112-118.
- Shiffrin, R.M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review*, 84, 127-190.
- Sillito, A.M., Jones, H.E., Gerstein, G.L., & West, D.C. (1994). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature*, 369, 479-482.
- Simon, J.R., & Rudell, A.P. (1967). Auditory S-R compatibility: The effect of an irrelevant cue on information processing. *Journal of Applied Psychology*, 51, 300-304.

Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. Brain, 120, 535-559.

- Taylor, J.L., & McCloskey, D.I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology*, 63, 439-445.
- Taylor, J.L., & McCloskey, D.I. (1996). Selection of motor responses on the basis of unperceived stimuli. *Experimental Brain Research*, 110, 62-66.
- Tucker, M., & Ellis, R. (1998). On the relation of seen objects and components of potential action. Journal of Experimental Psychology: Human Perception and Performance, 24, 830-846.
- Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. Proceedings of the National Academy of Sciences of the United States of America, 100, 6275-6280.
- Weiskrantz, L., Warrington, E.K., Sanders, M.D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, 94, 709-728.

CHAPTER 2 STUDY 1: On-line control of pointing is modified by unseen visual shapes¹

2.1 Introduction

Most of us behave in our everyday life as though our limb actions are under our conscious control at all times. In fact, when brain pathology, trauma, or disease cause limb actions to occur that are not intended, neurologists provide special designations, such as <u>dystonia</u> for chronic involuntary movements (Berardelli et al., 1998), <u>apraxia</u> for a reduced ability to make voluntary movements, (Hermsdorfer et al., 1999) and <u>alien hand syndrome</u> for movements that seem to be controlled by an outside force (Parkin & Barry, 1991; Feinberg et al., 1992). Here we examine the possibility that some visually guided actions, even in healthy adults, are controlled by events that are never experienced at a conscious level.

The question of whether visually guided actions can be controlled by events outside of awareness poses a considerable challenge to the researcher. First, an experimental protocol is required in which visual events are presented that, on the one hand, are intense enough to influence brain processes in the participant, but on the other hand, do not result in explicit awareness of these events. Second, these subliminal events must be shown not only to influence visual processes, but also to influence motor action. Finally, it is not enough to show that motor responses are merely influenced by subliminal events; this could come about by the initiation (priming) of a response that has already been consciously prepared. For example, as a consequence of the instructions provided, an action plan may be established and the participant may use the subliminal information to initiate the preprogrammed response. Thus, to show that visually guided actions can be controlled by subliminal events, it is necessary to show that the priming occurs while motor actions are ongoing. This was the challenge we set for ourselves in the present study.

An established method for presenting subliminal shapes to participants is through the psychophysical procedure of metacontrast masking (for reviews see Kahneman, 1968; Breitmeyer, 1984; Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000). This is a form of

¹ A version of this chapter has been accepted for publication.

Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006b). On-line control of pointing is modified by unseen visual shapes. *Consciousness and Cognition*, in press.

backward masking in which the visibility of a briefly displayed shape (called the <u>prime</u>) is greatly reduced when it is followed by another shape that fits snugly around the first shape but does not touch it (called the <u>mask</u>). By varying the amount of time that passes between the onset of the prime and the mask, the prime can be rendered invisible to the system responsible for conscious reports and discrimination; prime visibility is typically lowest when the interval is between 40-80 ms (Breitmeyer, 1984). Studies have shown that even under circumstances in which prime shapes cannot be discriminated above a chance level, these unseen prime shapes still influence motor responses that are made to the visible mask that follows in time. Both simple and choice response times to the mask are faster when it is preceded by a prime that shares attributes critical to the correct response (Taylor and McCloskey, 1990, 1996; Klotz and Neumann, 1999; Ansorge et al., 2002).

But are these responses to the mask reflecting a direct subliminal influence on an ongoing action? Or is the influence on the initiation of an already-prepared action? In a recent study designed to document direct subliminal influences on the on-line control of action, Schmidt (2002) modified a metacontrast masking procedure so that his participants made short aiming movements in response to the colour of the mask (instead of the usual presses on keys in fixed locations). Red and green prime disks were first presented simultaneously in opposite quadrants of a screen, 32 mm away from a central fixation point. These prime disks were displayed for 10 ms and then masked by red and green annuli (rings) that appeared 10 to 60 ms after the onset of thee primes. At each prime location, the annulus colour was either the same as the previous prime (an example of a <u>congruent trial</u>, in which the prime and mask indicated the same response was required) or opposite (an example of an <u>incongruent trial</u>, in which the mask indicated the alternative response to that initially specified by the prime was required). Participants were instructed to move their finger quickly and accurately from the central home position to the annulus with a pre-specified colour (e.g., red).

Despite the fact that the prime disks were masked so that their colour could only be correctly discriminated 55 to 65% of the time (chance = 50%), Schmidt reported that motor responses to the mask were strongly influenced by location of the red prime disk. Participants tended to begin their movements approximately 230 ms after prime onset, regardless of the prime-mask onset asynchrony. Most importantly, these movements initially

began in the direction of the red prime disk and so were slower to complete on incongruent trials (when the red mask annulus appeared in another location) than on congruent trials (when the red mask annulus was in the same location). A kinematic analysis revealed that these movement trajectories were modified while the finger was in flight, with noticeable corrections on incongruent trials and a single fluid limb motion on congruent trials.

Schmidt's (2002) results clearly show that the colour of the subliminal prime disks influenced the trajectory of a limb movement. However, it is not clear that this influence was on the on-line control of action, as claimed. Instead, it is possible that only the initiation of the response (e.g., move to the red location) was influenced by the prime, with the decision to initiate the movement on the basis of the prime leading to more rapid success on congruent trials and less direct success on incongruent trials. If so, the effects of the prime were on movement initiation not on the control of ongoing action.

This leaves us with the question of whether subliminal shapes can influence the online control of action, specifically whether they can influence an action after a different action has already been initiated. To address this question we modified Schmidt's (2002) procedure such that the critical prime-mask sequence was presented after the initiation of a goal-directed movement. The sequence of events is illustrated in Figure 1. Participants were given a fixed movement goal, to complete a rapid movement to a center target location. On 75% of trials, they simply performed the task of pointing to a target shape that appeared in the center of the display. However, on 25% of trials, a directional arrow prime-mask sequence was presented in the center location. This directional mask was the signal for participants to modify their pointing movement so that their finger landed in either the left or the right eccentric target location, according to the direction indicated by the mask.

We reasoned that if masked primes could influence the on-line control of a goal directed movement we would observe deviations in movement trajectories that corresponded to the identity of the unseen primes shortly after the onset of those primes. Furthermore, there should be a difference in the trajectories observed for congruent and incongruent primemask pairs. On the other hand, if masked primes are only able to influence the initiation of an already prepared action then deviations in the movement trajectories should only be seen in response to the direction indicated by the visible mask. Congruent versus incongruent prime-mask pairs should then not have any influence on movement trajectories.

2.2 Method

2.2.1 Participants. Eleven right-handed university students (7 female, 4 male, mean age = 21.9 ± 2.2 years) with normal or corrected-to-normal visual acuity participated in this study. Participants were paid \$20 for their involvement. All participants gave informed consent, and the study was conducted in accordance with the ethical guidelines set by the University of British Columbia. Data from one participant were excluded for failure to follow task instructions.

2.2.2 Apparatus. Shapes were presented in white on a black background (Viewsonic 19" monitor, 70 Hz refresh), oriented 20 degrees from the horizontal. Participants viewed the display from a distance of approximately 60 cm, with their head movements restricted by a chin-rest. The participants were positioned such that their midline was aligned with the center of the display and a home position (demarcated by a 12 mm circular marker) located centrally at the bottom of the display. In all tasks, stimuli were presented in the center of the display, located 27.0 cm directly above the home position. A DOS-based microcomputer was used to control stimulus presentation and data collection.

2.2.3 Stimuli. Prime shapes (4 mm x 9 mm) consisted of a left-pointing and right-pointing arrow, as well as a neutral shape formed from the superimposition of the two arrows. Masks consisted of larger (23 mm x 28 mm) versions of the same shapes as the primes, with a central cutout (see Figure 1). The outer contour of the prime stimuli fit exactly within the inner contour of the central cutout of the masks. In all trials, primes were presented for 14 ms and the prime-mask stimulus-onset asynchrony (SOA) was set at 56 ms. The SOA duration was selected based on pilot experiments demonstrating that it produced the strongest metacontrast masking. Masks were presented at the same central position as the primes until the pointing response was complete (approximately 400 ms).

2.2.4 Movement Analysis. Participants performed the pointing task with a stylus in their right hand. An infrared-emitting diode was placed at the tip of the stylus and 3D position was monitored using an OPTOTRAK (Northern Digital, Waterloo, Ontario) motion analysis system (spatial resolution 0.01 mm). The tip of the stylus was equipped with a microswitch that provided an analog signal indicating whether or not the stylus was in contact with the surface of the display. The 3D position of the stylus and the status of the microswitch were

sampled at 500 Hz. Raw data from the OPTOTRAK were converted into 3D coordinates and digitally filtered using a second order dual-pass Butterworth filter with a low-pass cutoff frequency of 10 Hz. The start and end of the movement was determined by the status of the stylus miscroswitch.

÷4. 4.

2.2.5 Procedure. Participants completed three tasks in a single experimental session. First, they performed the <u>Mask Response Time</u> task. Participants rested their left and right index fingers on the left "z" key and right "/" key of a standard keyboard, respectively. The keyboard was centered on the home position. Participants were instructed to direct their attention to a fixation point at the center of the display monitor (500-1000 ms) and respond as quickly and as accurately as possible to the direction of the mask arrow (left or right) with the corresponding key press. Mask arrows were preceded by a left pointing, right pointing, or neutral prime arrow (14 ms). Prime-mask SOA was 56 ms. Participants completed a single block of 120 trials.

Participants then performed the <u>Mask Pointing</u> task, which involved making pointing movements from a home position to a center square target $(3.3 \text{ cm}^2) 27.0 \text{ cm}$ away. The center target was flanked on each side by square targets such that the distance between the middle of the center target and the left or the right target was 7.0 cm. Participants could begin their movement to the center target anytime following the appearance of the target boxes (with no reaction time constraints). On 75% of the trials (direct pointing), movement of the stylus initiated the appearance of the neutral prime shape (14 ms) followed by a neutral mask shape (SOA = 56 ms) in the center target box. Participants were instructed that when this neutral mask shape appeared they were to continue pointing to the center target with a movement time goal of 300-500 ms. On the remaining 25% of trials (perturbed pointing), the prime was one of three shapes (left arrow, right arrow, neutral shape) and the mask in the center box was either a left or a right pointing arrow. Participants were instructed that the mask arrow was a signal to modify their pointing movement to the center box and to complete their point by landing in the box indicated by the mask arrow.

Participants began with 20 practice trials of direct pointing. They then completed 2 blocks of 240 test trials in which the 75% of direct pointing trials were randomly interspersed with the 25% of perturbed pointing trials. Movement time was measured from stylus lift-off

to stylus contact with one of the target boxes. Participants were given a movement time goal of 300-500 ms and movement time feedback was provided following all direct pointing trials.

The final task performed by all participants was <u>Prime Identification</u>. Participants were told that one of three prime shapes would be presented randomly on each trail and their task was to identify them by making a 3-alternative forced choice. They were also told that only accuracy was being measured and that response speed was no longer important. The display sequence was identical to the mask pointing task. Participants viewed the prime-mask sequence with their right index finger resting on the space bar. A tone sounded 400 ms following the mask, indicating that the participant could respond by pressing the left key (b), the center key (n), or the right key (m) with their right index finger to indicate a left pointing, neutral or right pointing prime arrow, respectively. Each participant completed 120 trials.

2.3 Results

Prime Identification: Primes were barely visible to participants.

At the beginning of the prime identification task, all participants were surprised to learn that mask arrows had been preceded by prime arrows. These subjective reports were confirmed by their performance in the prime discrimination task. Chance performance in this task was 33% (given the three equally likely alternatives). Mean accuracy collapsed across all prime-mask sequence combinations was $39.67\% \pm 17.16$ (SD), which differed significantly from the chance level of 33.3% at the p < .05 level, but not at the p < .01 level, t(1,9) = 2.7. This is less than the level of visibility reported by Schmidt (2002), where accuracy was at 60% and chance was 50%.

We also noted that prime accuracy differed significantly, depending on the relation between prime and mask. Mean accuracy on neutral prime and incongruent prime-mask trials did not differ significantly from the chance level of 33% (neutral prime: $\bar{x} = 31.8\%$, t(9) < 1, incongruent prime: $\bar{x} = 34.5\%$, t(9) < 1), but mean accuracy on congruent primemask trials was significantly greater (52.8%, t(9) = 4.60, p = .001). A data pattern like this has been attributed to a biasing influence of the visible mask on reports of the prime rather than a true measure of prime visibility (Vorberg et al., 2003).

Mask Response Time: Invisible primes influence response selection.

Participants were very accurate in the mask response time task (> 97% correct overall) and mean correct response times $(RT)^2$ with respect to the neutral prime trials are shown in Figure 2. In addition to the difference scores displayed in Figure 2, the RTs for all prime-mask trial combinations are provided in Table 1. The influence of the prime arrows on these responses can be seen in the large statistical interaction between prime and mask shapes, F(2,18) = 128.761, p < .001. Post hoc mean comparisons (Tukey HSD) revealed that RT was smaller when masks were preceded by congruent primes than by either incongruent (p < .05) or neutral primes (p < .05). Furthermore, mean RT was larger for incongruent displays than for neutral displays (p < .05). This replicates the previously reported finding that invisible primes influence choice response times to the identities of similar looking masks (Taylor and McCloskey, 1990, 1996; Klotz and Neumann, 1999; Ansorge et al., 2002).

Mask Pointing: Invisible primes influence the on-line control of action.

Participants were able to complete the movement to the center target on direct pointing trials within the required movement time ($\bar{x} = 392 \text{ ms} \pm 40.5 \text{ SD}$). When the directional masks appeared on perturbed trials, participants were able to successfully modify their movements and land in the appropriate eccentric target on the majority of trials ($\bar{x} =$ $86.1 \% \pm 18.1 \text{ SD}$). On the 14% of perturbed trials on which participants failed to modify their pointing correctly, their fingers always landed in the center target within the movement time goal. However, this error occurred less frequently when a directional prime preceded the directional mask (congruent = $8\% \pm 12.4 \text{ SD}$; incongruent = $7\% \pm 7.3 \text{ SD}$), than when a neutral prime preceded the directional mask ($\bar{x} = 26\% \pm 23.9 \text{ SD}$, F(2,18) = 9.738, p = .001). This is therefore initial evidence that the prime shape (in this case the neutral prime) influenced the ultimate target of the pointing action.

Movement time (MT) on corrected perturbed trials, with respect to perturbed trials in which the neutral prime was displayed, is shown in Figure 3 and MT for all prime-mask combinations provided in Table 1. In addition to the error results, the MT results indicate

 $^{^{2}}$ In all other chapters, the term response time (RT) has been replaced with reaction time (RT).

that the prime-mask relationship influenced the pointing response, F(2,18) = 39.52, p < .001) (see Figure 3). Post-hoc tests (Tukey HSD, p < .05) indicated that participants were faster to complete movements to an eccentric target when the directional mask was preceded by a congruent than an incongruent prime. The difference in movement time between incongruent and neutral primes was not significant. These results indicate that the primes were having an influence on the overall time required to complete a successful pointing modification.

But at what point in the ongoing pointing action did the primes begin to have an influence? To examine this question, we compared pointing trajectories for the perturbed trials in which participants moved to the correct eccentric target to an average spatial trajectory computed for the direct pointing trials. The average spatial trajectory in the 2D plane was calculated for each participant from all direct pointing trials in the 2 testing blocks. The points in this trajectory were obtained by deriving the mean lateral spatial position in the x-y plane for every 2 mm of forward movement progression. If a trajectory did not have a position value at the exact spatial location required, one was obtained by linear interpolation from the closest data points within a maximum distance of 1 mm. In addition, the standard deviation of the mean position in the x-direction was also calculated. The resulting mean spatial trajectory, together with its 2 standard deviation bandwidth, then became the standard against which pointing on perturbed trials were assessed (see Cressman et al., 2006).

Figure 4 illustrates a mean spatial trajectory, computed from the direct pointing trials, and individual perturbed trials in which a participant responded to a left pointing arrow mask and landed in the left target. From the mean path displayed (open circles) it appears that the trajectories on direct trials move in a fairly straight line toward the center target box. In contrast, the trajectories on perturbed trials differed substantially from the direct pointing trials and from each other depending on the shape of the prime displayed. In the perturbed pointing trials (solid lines), trajectories initially deviated in the direction of the prime, regardless of the mask displayed. Thus there was no inhibition, as the primes activated a response directly. Pointing modifications to the left goal target were made earlier for congruent primes than neutral primes, and pointing modifications were initially made in the wrong direction for incongruent primes.

To examine these differences in movement perturbations, a conservative estimate of the time at which the movement began to deviate toward the target specified by the mask (i.e. left target) was calculated. This estimate was defined as the point in time at which displacement in the horizontal axis of the movement reached a maximal value and showed a reversal toward the appropriate eccentric target. These mean estimates, with respect to perturbed trials in which the neutral prime is displayed, are shown in Figure 5 and mean values provided for all prime-mask congruencies provided in Table 1. The time at which the movement began to deviate toward the target specified by the mask is dependent on prime-mask congruency (F(2,18) = 86.188, p < .0001). Tukey HSD analyses revealed that modifications to congruent primes occurred earlier than to incongruent or neutral primes (p < .05), with no difference between incongruent and neutral primes.

An examination of the lateral displacement made in completing the pointing movement to the eccentric target from the point in the trajectory at which the pointing modification had begun showed that participants made shorter movements when the prime was congruent ($\bar{x} = 70.0 \text{ mm} \pm 15.3 \text{ SD}$) or neutral ($\bar{x} = 70.7 \text{ mm} \pm 13.0 \text{ SD}$) than when it was incongruent ($\bar{x} = 79.2 \text{ mm} \pm 14.9 \text{ SD}$), F(2,18) = 19.886, p < 0.001. Yet, at the same time, the total movement time in the incongruent and neutral conditions were not different from one another. To examine how this came about, we explored the possibility that participants completed the late portion of the trajectory more quickly when the primes were incongruent than when they were neutral. An analysis of the peak lateral velocity during this final trajectory segment revealed that this was indeed the case, F(2,18) = 13.771, p = .001. On average, participants reached greater peak velocities during this final movement segment when the prime and mask were incongruent ($\bar{x} = 533.3 \text{ mm/s} \pm 64.8 \text{ SD}$) than when they were congruent ($\bar{x} = 475.7 \text{ mm/s} \pm 38.9 \text{ SD}$) or neutral ($\bar{x} = 478.9 \text{ mm/s} \pm 31.8 \text{ SD}$).

2.4 Discussion

The goal of the present experiment was to determine if subliminal shapes are capable of influencing the on-line control of action. To address this question, we used a metacontrast masking procedure in which the critical prime-mask sequence was presented after the initiation of an already-prepared target-directed movement. As a comparison with previous findings, we also required participants to complete a choice response time task in which the prime-mask sequence was presented prior to the selection and initiation of discrete key press responses. Finally, we required participants to perform a perceptual discrimination task, in which they attempted to identify the masked primes. These procedures allowed us to demonstrate three important findings.

First, we established that the prime shapes in our procedure remained inaccessible to participants' conscious awareness. This replicates numerous previous studies of masked priming. Second, we demonstrated that invisible primes influence the latency of motor responses in the choice response time task, as previous studies have also shown (Taylor and McCloskey, 1990, 1996; Neumann and Klotz, 1994; Ansorge et al., 2002; Breitmeyer et al., 2004). Third, and most important for the goal of our study, we showed that these same subliminal shapes not only can influence the speed with which a goal-directed action is initiated, as in previous studies (Schmidt, 2002), but they can influence the control of ongoing action.

The novel contribution of this study is that it showed the influence of invisible primes for ongoing goal-directed actions, rather than merely in the initiation of these actions. The main evidence for this was that initial deviations in movement trajectories from the center target were always in the direction cued by the prime, regardless of the direction of the subsequent mask. Participants did not wait for information from the mask before they began to modify their movements. Thus congruent primes gave the pointing modification a head start in the correct direction, with modifications occurring within 277 ms of movement onset. In contrast, incongruent primes resulted in initial trajectory deviations toward the wrong target. Consequently, additional movement time was required for participants to correct the movement. Pointing trajectories were not directed to the correct target until participants had reacted to the mask, approximately 330 ms into the movement. When a neutral prime preceded the directional mask, participants adjusted their trajectories in response to the mask at latencies similar to those observed in incongruent prime trials, as in both incongruent and neutral perturbed trials the movement goal was not specified until the mask was displayed. The difference in movement correction latencies between congruent (277 ms) versus incongruent and neutral (330 ms) prime-mask trials was approximately equal to the prime-

mask SOA (56 ms). This suggests that new pointing-relevant visual information is incorporated into control of the pointing action as soon as it becomes available.

Taken together, the difference in the latency of trajectory modifications to the correct eccentric target in congruent trials compared to incongruent and neutral prime trials, as well as the short latency of these pointing modifications, suggest that participants processed and responded to the primes and masks in feed-forward manner. Movement trajectories to the center target were modified on-line, first in response to the invisible prime and then if necessary, in response to the visible mask. Thus, we can be confident in this study that the prime did not influence the initiation of an already-prepared movement. Rather, the primes influenced the on-line control of a goal-directed action. Furthermore, the prime's influence appears to have been automatic, as defined by previous research examining the ability to make rapid, on-line adjustments in limb movements in response to unexpected changes in the location, shape and orientation of a target object (e.g., Bard et al. 1999; Brenner and Smeets 2003; Cressman et al., 2006; Desmurget and Prablanc 1997; Desmurget et al. 1999; Paulignan et al. 1991; Pisella et al. 2000; Prablanc et al. 1986).

The automatic influence of invisible primes on an ongoing visually guided action can best be characterized within Neumann's theory of <u>direct parameter specification</u> $(DPS)^3$ (Neumann, 1990; Neumann and Klotz, 1994). According to DPS, there is a direct link between sensory information and the response parameters concerning when and how to respond, which does not require mediation by conscious processes. For example, as a consequence of instruction, action planning takes place and a conditional readiness is established. Visual information can be fed into the motor system without reaching conscious awareness. A response is activated if the sensory related activity contains relevant features critical to a given response.

DPS can readily account for most features of the priming effects we observed in both our response time and pointing tasks. Specifically, when prime and mask were congruent, responses were fastest in the response time task and pointing trajectories deviated earliest to the correct target in the pointing task. However, there is one difference in the pattern of

³ In all other chapters, theories put forth to explain how subliminal stimuli influence action are referred to collectively as adopting a top-down contingency framework. Neumann's (1990) theory of Direct Parameter Specification is the first theory to suggest that the influence of subliminal stimuli on action is guided by one's intentions.

participants' responses between the two tasks that DPS does not readily explain. In the response time task, participants' first recorded response was almost always consistent with the identity of the mask and not of the prime (accuracy was above 97% in that task). In contrast, when participants were pointing based on the masks, the first recorded responses (trajectory deviations) were observed in the direction of the prime, whether or not the prime was congruent with the subsequent mask. Thus, participants in the choice response time situation appeared to have waited until they identified the mask before committing to an overt response. They did not make an observable response to the identity of the prime in the response time task as they did in the pointing task (cf. Schmidt, 2002). This is likely why the neutral prime RTs are more similar to the congruent MTs in the choice response task and why the neutral MTs are more similar to the incongruent MTs in the pointing task; actions in the choice task must be withheld until the final mask information is available whereas in the pointing task there is no obvious penalty for a premature deviation in the direction of the prime.

This difference in response patterns for the two tasks suggests that there is flexibility in the way subliminal information is used for the control of action. At this point we can only speculate on how this flexibility in visuomotor processing is accomplished. One possibility in keeping with DPS theory (Neumann, 1990; Neumann and Klotz, 1994) is that of a fluctuating motor activation threshold. The level of this threshold could be strategically set at different levels, depending on task constraints. In a pointing task such as the one studied here, and in Schmidt's (2002) response time task, participants are able to correct initial response errors and still complete the task successfully, regardless of initial deviations from the immediate action goal. For this reason, a lower activation threshold could be set, allowing prime-related activity to influence responses with little to no monitoring. In contrast, in the choice response time task, the penalty of pressing the incorrect key would prompt the setting of the activation threshold at a higher level. We offer this account of the differences between the two tasks as a working hypothesis. Future experiments will be needed to fully explore the flexibility in prime activated responses. For now, the results show conclusively that masked shapes can influence both response initiation and the on-line control of goal-directed actions in the absence of conscious awareness.

2.5 Bridging Summary

In Study 1 we have demonstrated that invisible primes can influence the on-line control of a goal-directed action, such that trajectories are modified in response to unconscious visuomotor processes. Furthermore, we have speculated that these trajectory deviations arise automatically. According to the dual systems theory of visual processing (see Milner and Goodale, 2005), automatic visuomotor transformations arise as a result of processes occurring in the dorsal visual stream. Specifically, the dual systems theory of visual processing proposes that visual information is processed in two parallel streams; a ventral stream which gives rise to conscious perception and a dorsal stream responsible for the automatic on-line guidance of motor behaviour. Consequently, we have implied that the impact of primes on action, as observed in Study 1, arises due to processes occurring in the dorsal visual stream.

In accordance with this proposal, previous research investigating the phenomenon of masked priming has suggested that the dissociation between perception and action observed in metacontrast masking RT tasks can be accounted for by processes occurring in the two separate visual streams. For example, the unconscious visuomotor processing of masked primes for the control of action could be a signature of the operation of the dorsal visual stream, while the primes are made unavailable for conscious report due to processes occurring in the ventral stream. However, previous metacontrast masking RT tasks investigating masked priming have typically not been designed to be conducive to dorsal stream processing. Furthermore, it is questionable if any reaction time results can or should be attributed to processes occurring in a visual stream specialized for the on-line control of action. Finally, the results of Study 1 do not dictate that the influence of the primes on action arose due to exclusive dorsal stream processes.

Thus, in order to determine if the influence of a subliminal prime on action during a goal-directed movement arises (automatically) as a result of dorsal stream processes, the present study investigated the influence of prime stimuli on rapid visually-guided actions whose characteristics were particularly suited for dorsal stream control (see Pelisson et al., 1986; Desmurget et al., 1999; Pisella et al., 2000). Participants reacted as quickly as possible to the onset of 3 target boxes and performed a rapid pointing movement to the center target (movement time goal = 300 ms). As in Study 1, a directional mask arrow was the signal for

participants to modify their initial trajectories and complete the movement to the corresponding eccentric target. Masks were preceded by a prime stimulus, consisting of a left or right pointing arrow prime or a neutral shape. In contrast to Study 1, the prime-mask sequence was displayed randomly, either during the reaction time interval or upon movement onset. If the influence of a prime on action does indeed arise automatically as a result of dorsal stream processes, we expected to observe similar modifications in trajectories in the direction of the prime in the current investigation, as those obtained in Study 1.

2.6 Table

Table 2.1. Mean (SE) response times (ms), pointing movement times (ms) and times of finaltrajectory modifications in the goal-directed movement.

	Congruent Prime-Mask	Incongruent Prime-Mask	Neutral Prime- Directional Mask
Response Time (ms)	333.2 (9.5)	389.9 (7.1)	348.6 (9.2)
Pointing Movement Time (ms)	515.0 (12.1)	571.7 (10.9)	581.8 (11.9)
Final Trajectory Modification (ms)	277.3 (4.4)	333.0 (4.6)	321.6 (4.1)

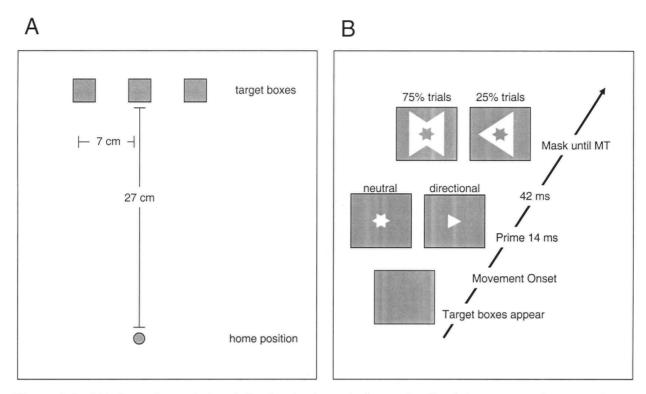
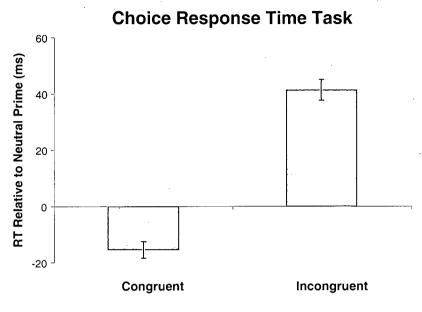
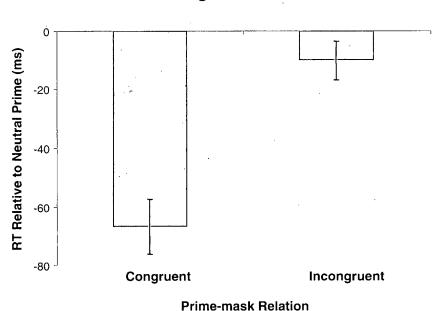


Figure 2.1. (A) Overview of visual display in the pointing task. Participants were instructed to make a pointing movement from the home position to the center target box with a movement time goal of 300-500 ms. Directional arrows cued participants to modify their movements to the center target and land in either a left or right eccentric target. (B) Temporal sequence of a direct pointing trial (left) and a perturbed pointing trial (right). In the pointing task, 75% of the trials were cued responses to the central target (neutral prime + neutral mask). On the remaining 25% of trials, participants had to modify their final movement goal in the direction specified by the mask (left or right). The prime-mask sequence was displayed upon movement onset.



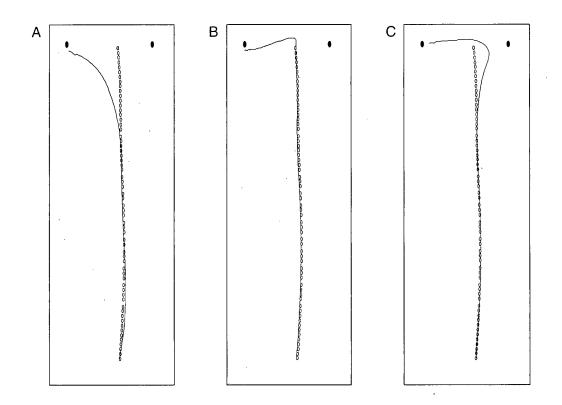
Prime-mask Relation

Figure 2.2. Effect of prime-mask congruency on choice response times (RT) to the mask stimulus. Results are shown for congruent and incongruent prime-mask combinations with respect to mean performance on trials in which a neutral prime was displayed. Note: a negative score indicates responses were initiated faster than when a neutral prime was displayed, whereas a positive score indicates performance was slower. Error bars denote standard errors. A breakdown of the choice RTs are provided in Table 1.

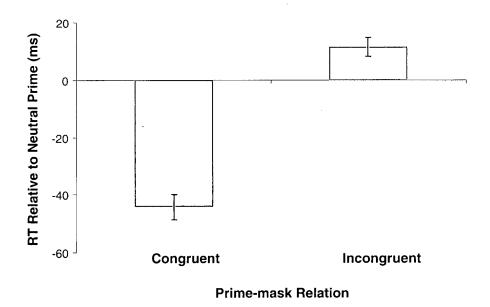


Pointing Movement Time

Figure 2.3. Movement times (MT) to eccentric targets with respect to mean performance on trials in which a neutral prime preceded the directional mask. A negative score indicates a faster movement was completed to the eccentric target than when a neutral prime was displayed and a positive score indicates a slower movement. Error bars denote standard errors. A breakdown of MTs are provided in Table 1.



<u>Figure 2.4.</u> Examples of mean direct spatial trajectories (open circles) and individual perturbed spatial trajectories (solid line) under each of the three conditions in which a left directional mask was displayed ((A) congruent prime, (B) neutral prime or (C) incongruent prime). The center of the eccentric target boxes are indicated by annuli (the center target box is not visible). Note the early trajectory deviation to the left eccentric target in the congruent trial and the initial incorrect trajectory deviation in the incongruent trial.



Final Trajectory Modification

Figure 2.5. Latencies of final trajectory reversal, at which point participants began to move to the eccentric target cued by the directional mask, with respect to mean performance on trials in which a neutral prime preceded the directional mask. A negative score indicates a movement was initiated earlier to the eccentric target than when a neutral prime was displayed, whereas a positive score indicates the modification in trajectory occurred at a later point in time. Error bars denote standard errors. A breakdown of the results are provided in Table 1.

2.8 References

- Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-545.
- Bard, C., Turell, Y., Fleury, M., Teasdale, N., Lamarre, Y., & Martin, O. (1999).
 Deafferentation and pointing with visual double step perturbations. *Experimental Brain Research*, 125, 410-416.
- Berardelli, A., Rothwell, J.C., Hallett M., Thompson, P.D., Manfredi, M., & Marsden, C.D. (1998). The pathophysiology of primary dystonia. *Brain*, 121, 1195-1212.
- Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.
- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1595.
- Brenner, E., & Smeets, J.B. (2003). Perceptual requirements for fast manual responses. *Experimental Brain Research*, 153, 246-252.
- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006). No automatic pilot for visually guided aiming based on colour. *Experimental Brain Research*, 171, 174-183.
- Desmurget, M., & Prablanc, C. (1997). Postural control of three-dimensional prehension movements. *Journal of Neurophysiology*, 77, 452-464.
- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E. & Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2, 563-567.
- Enns, J.T., & DiLollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Breitmeyer, B.B., Ro, T., & Singhal, N.S. (2004). Unconscious color priming occurs at stimulus- not percept- dependent levels of processing. *Psychological Science*, 15, 198-202.
- Feinberg, T.E., Schindler, R.J., Flanagan, N.J., & Haber, L.D. (1992). Two alien hand syndromes. *Neurology*, 42, 19-24.
- Hermsdorfer, J., Ulrich, S., Marquardt, C., Goldenberg, G., & Mai, N. (1999). Prehension with the ipsilateral hand after unilateral brain damage. *Cortex*, 35, 139-161.

Kahneman, D. (1968). Methods, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70, 404-425.

- Klotz, W., & Neumann, O. (1999). Motor activation without conscious discrimination in metacontrast masking. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 976-992.
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-215.
- Neumann, O., & Klotz, w. (1994). Motor responses to nonreportable, masked stimuli:
 Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Parkin, A.J., & Barry, C. (1991). Alien hand sign and other cognitive deficits following ruptured aneurysm of the anterior communicating artery. *Behavioural-Neurology*, 4, 167-179.
- Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements 1. The effects of changing object position. *Experimental Brain Research*, 83, 502-512.
- Pisella, L., Gréa, H., Tilikete, C, Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729-736.
- Prablanc, C., Pélisson, D., & Goodale, M.A. (1986). Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research*, 62, 293-302.
- Schmidt, T. (2002). The finger in flight: Real-time motor control by visually masked color stimuli. *Psychological Science*, 13, 112-118.
- Taylor, J.L., & McCloskey, D.I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology*, 63, 439-445.
- Taylor, J.L., & McCloskey, D.I. (1996). Selection of motor responses on the basis of unperceived stimuli. *Experimental Brain Research*, 110, 62-66.

Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. Proceedings of the National Academy of Sciences of the United States of America, 100, 6275-6280.

CHAPTER 3

STUDY 2: Can the processing of visually-masked stimuli during rapid target-directed actions be mediated by the dorsal stream?⁴

3.1 Introduction

Visuomotor processing in the absence of conscious awareness is readily demonstrated in a metacontrast dissociation paradigm. Previous investigations using this type of paradigm have typically employed a choice reaction time (RT) task in which participants are instructed to press either a left or right key in response to a particular attribute of the target stimulus. For example, participants may be instructed to press a left or right key in response to a left or right arrow target (*the mask*), respectively (see Vorberg et al., 2003). Unbeknownst to the participants, the masks are preceded by a prime stimulus that is rendered invisible to the conscious system as a result of metacontrast masking; a form of backward masking in which the visibility of a briefly displayed stimulus (the prime) is greatly reduced when it is followed by a spatially flanking stimulus (the mask) (for reviews of metacontrast masking see: Kahneman, 1968; Breitmeyer, 1984; Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000). Despite the inability of participants to consciously detect the primes or discriminate between them in a perceptual identification task, the unseen primes influence motor responses to the visible mask that follows in time. Specifically, both simple and choice reaction times to the mask are faster when the mask is preceded by a prime that shares attributes critical to the correct response (congruent trial) compared to a neutral stimulus. In contrast, if the mask is preceded by a prime that shares attributes critical to the alternative response (incongruent trial), response times to the mask are slower compared to the same neutral stimulus (Taylor and McCloskey, 1990, 1996; Klotz and Neumann, 1999; Ansorge et al., 2002).

The ability of a prime to influence action, in the absence of awareness, raises the possibility that the visuomotor processing of the prime stimulus may be independent of the processes responsible for forming a conscious percept. In line with this proposal several researchers have interpreted their results based on Milner and Goodale's dual systems theory of visual processing (Goodale and Milner, 1992; Milner and Goodale, 1995). According to the dual systems theory, visual information is processed in two (functionally distinct) parallel

⁴ A version of this chapter will be submitted for publication.

streams; the ventral and dorsal visual stream. The ventral stream projects from visual cortex to the inferior temporal cortex (ITC) and is responsible for conscious perception and visual experience. The dorsal stream, or sensorimotor system, projects from visual cortex to the posterior parietal cortex (PPC) and is responsible for the on-line control of visually-guided actions. In contrast to the ventral stream, the dorsal stream is believed to operate automatically, outside of conscious awareness. Thus, researchers (e.g. Eimer and Schlaghecken, 1998; Schmidt, 2002; Jaskowski et al., 2003) have put forth that the processing of the prime in the dorsal stream is responsible for its influence on action, while the prime fails to reach conscious awareness because of distinct processes occurring in the ventral stream, and have discussed their results accordingly.

However, it is unclear if the perception-action dissociation observed in reaction time tasks employing metacontrast masking paradigms can (or should) be explained by Goodale and Milner's (1992) dual systems theory. Masked stimuli have been shown to influence responses across various stimulus attributes and response modes. For example, RT to the mask has been shown to be facilitated when the prime and mask share the same location (Ansorge et al., 2002), orientation (Vorberg et al., 2003), shape (Neumann and Klotz, 1994), colour (Schmidt, 2002; Breitmeyer et al., 2004) or semantics (Dehaene et al., 1998; Kunde et al., 2003). In addition, a similar benefit in reaction time is observed when participants are required to make a verbal response to the mask (e.g. utter the word left or right) as opposed to perform a manual key press (Ansorge et al., 1998). While the dorsal stream is thought to be capable of processing such attributes as object orientation, size and location for the on-line guidance of movements; proper shape recognition, semantic processing, and processes leading to verbal reports have typically been assigned to the ventral stream (e.g. Carey et al., 1996, Pisella et al., 2000).⁵ Hence, exclusive dorsal stream processing cannot be held

⁵ The ability of the dorsal stream to process colour for the immediate control of visually-guided action is currently debated. Results obtained by Brenner and Smeets (2004), Schmidt and colleagues (Schmidt, 2002; Schmidt et al., 2006, Vath and Schmidt (2007)) and White et al. (2006) suggest that colour can be processed by the dorsal stream for the immediate control of action. In line with this proposal, Toth and Assad (2002) have demonstrated that the parietal cortex can selectivity code for a specific visual feature (e.g. colour), when it is relevant to the task. In contrast, results obtained by Pisella and colleagues (2000; see also Cressman et al., 2006b) demonstrate that colour cannot be processed by the dorsal stream for the automatic guidance of pointing movements. The position of Pisella and Cressman is based on results obtained from an experimental paradigm employing a stop-command (e.g. participants are required to stop a goal-directed movement in response to a change in stimulus colour). In contrast, research demonstrating the ability of participants to use colour information for the automatic guidance of action typically employs a go-paradigm (e.g. participants are to move

accountable for the influence of primes on action observed in all metacontrast masking RT paradigms performed to date. Moreover, it is questionable if any RT results should be attributed to processes occurring in a visual stream specialized for the on-line control of action. According to recent work by Adam and Pratt (2004), RT tasks in which participants are required to select a limb in order to initiate the appropriate response, may engage separate mechanisms from those utilized in the on-line control of action.

7

The purpose of the present experiment was to determine if the unconscious visuomotor processing of a prime stimulus could be a signature of the operation of the dorsal visual stream. In order to achieve this goal, we examined the influence of prime stimuli on action in a task whose characteristics were particularly suited for dorsal stream control. Previous experiments examining visuomotor processing have suggested that dorsal stream processes underlie automatic modifications to unfolding movement trajectories in response to changes in the location, orientation or shape of a target object (e.g. Paulignan et al., 1991; Goodale and Milner, 1992; Milner and Goodale, 1995; Desmurget and Prablanc, 1997; Bard et al., 1999; Desmurget et al., 1999; Goodale and Milner, 2004; Goodale and Westwood, 2004). Specifically, modifications in trajectories observed in response to changes in the stimulus display for movements completed in 300 ms or less, are proposed to be mediated exclusively by the dorsal stream (Pisella et al., 2000).

Pisella and colleagues' (2000) contention that the dorsal stream mediates fast corrective processes (i.e. modifications in limb trajectories for movements completed within 300 ms or less) is founded on results obtained in a pointing paradigm in which instructions were manipulated to distinguish between intentional and automatic motor corrections. In particular, Pisella and colleagues (2000) instructed participants to point to a target that would occasionally jump to a second location upon movement initiation. Depending on instructional set, participants were either to (1) modify their movements and land at the new target position in response to a target jump (Location-Go instruction) or (2) stop their movements if a target jump was detected (Location-Stop instruction). Results indicated that participants corrected to the new target position for movements completed in 300 ms or less, regardless of instructional set. In contrast, patient I.G., with damage to the dorsal stream, did

to a new target location). Given the differences in paradigms employed, it is difficult to compare the two positions. This paper does not attempt to resolve this issue, but notes that the ability of colour information to be processed by the dorsal stream for the on-line control of action is dependent on task requirements.

not show corrections to the new target position when completing the task under the Location-Stop instructions. Furthermore, adjustments in pointing trajectories to the new target position by patient I.G. in the Location-Go task occurred only for movements completed with a movement time greater than 300 ms. Based on these results, Pisella and colleagues (2000) concluded that adjustments in limb trajectories in movements of 300 ms (or less) are automatic and due to exclusive dorsal stream processing. Modifications occurring at a greater latency allow other visual streams to participate in motor output, enabling the movement to be completed in accordance with one's intentions.

Thus, in the current research, in order to determine if the unconscious processing of a prime stimulus could be mediated by the dorsal visual stream, we examined the on-line influence of a prime stimulus presented during a fast goal directed movement. Specifically, participants reacted as quickly as possible to the onset of 3 target boxes and performed a rapid pointing movement to the center target with a movement time goal of 300 ms. If a directional mask arrow appeared, participants attempted to modify the initial trajectory and complete the movement to the corresponding eccentric target. Masks were preceded by a prime stimulus, consisting of a left or right pointing arrow prime or a neutral shape, and the prime-mask sequence was presented randomly either within the reaction time interval or upon movement onset.

Of particular interest was the influence of the primes on pointing trajectories. We have previously demonstrated that when masked primes are presented upon movement onset during a goal-directed pointing movement, trajectories deviate in the direction of the subliminal prime (see Cressman et al., 2006). In particular, we found that movement trajectories were adjusted in the direction of the prime before they were modified in the direction of the visible mask. In our previous experiment the movements were completed in 400+ ms and under the possible guidance of both ventral and dorsal stream processes. Thus, it is unclear if these initial deviations in trajectories in the direction indicated by the prime arose due to dorsal stream processing or were mediated by additional visuomotor processes (e.g. processes occurring within the ventral stream). Given the movement time goal of 300 ms and Pisella and colleagues' (2000) contention that dorsal stream processes mediate visuomotor transformations within this timeframe, similar adjustments in the present experiment would have been guided by dorsal stream processing. Hence, these results would

reveal that the unconscious visuomotor processing of a prime stimulus can be mediated by the dorsal stream. Alternatively, if trajectories were not modified in the direction of the prime when movements were completed in 300 ms, this would not exclude the possibility of dorsal stream processes mediating the effects of the prime on action. However, it would raise the possibility that the prime's influence on motor behaviour is mediated by additional visuomotor processes (possibly occurring in the ventral visual stream), as there would be enough time for these visuomotor transformations to influence movement.

The inclusion of trials in which the prime-mask sequence was presented within the reaction time interval allowed us to examine the nature of visuomotor transformations occurring before movement onset. Specifically, we were interested in determining if similar processes would be engaged when the prime-mask sequence was displayed within the RT interval compared to when the limb was in flight. The majority of research examining modifications in trajectories (as a result of dorsal stream control) have adopted paradigms in which the perturbation, indicating a change in trajectory, is presented at movement onset (see Goodale et al., 1986; Pelisson et al., 1986, Desmurget et al., 1999; Pisella et al., 2003). Thus dorsal stream processing has typically been assigned responsibility for the automatic on-line control of visually guided actions once movements have been initiated. However, recent findings by Westwood and Goodale (2003), suggest that the dorsal stream may become engaged for the control of action once a response is cued, if the visual target is available. If the dorsal stream is indeed engaged for action control once a response is cued, and can process a subliminal prime for action, we would expect to see a similar influence of the prime on action, regardless of the time of stimulus presentation.

3.2 Method

3.2.1 Participants. Twelve right-handed university students (8 female, 4 male, mean age = 21.8 ± 2.6 years) with normal or corrected-to-normal visual acuity participated in this study. Participants were paid \$20 for their involvement. All participants gave informed consent, and the study was conducted in accordance with the ethical guidelines set by the University of British Columbia. Data from one participant were excluded for failure to follow task instructions.

3.2.2 Stimulus Display. Shapes were presented in white on a black background (Viewsonic 19" monitor, 70 Hz refresh), oriented 15 degrees from the horizontal. Participants viewed the display from a distance of approximately 60 cm, with their head movements restricted by a chin-rest. The participants were positioned such that their midline was aligned with the center of the display and a home position (demarcated by a 12 mm circular marker) located centrally at the bottom of the display. In all tasks three possible targets (target = 3.3 cm^2) were displayed and stimuli were presented in the center target. The center target was located 27 cm directly above the home position. It was flanked on each side by similar square targets such that the distance between the middle of the center target and the left or the right target was 7.0 cm. A DOS-based microcomputer was used to control stimulus presentation and data collection.

3.2.3 Stimuli. Prime shapes (4 mm x 9 mm) consisted of left-pointing and right-pointing arrows, as well as a neutral shape formed from the superimposition of the two arrows. Masks consisted of larger (23 mm x 28 mm) versions of the same shapes as the primes, with a central cutout (see Figure 1). The outer contour of the prime stimuli fit exactly within the inner contour of the central cutout of the masks. In all trials, primes were presented for 14 ms and the prime-mask stimulus-onset asynchrony (SOA) was set at 56 ms. Masks were presented at the same central position as the primes until the pointing response was complete (approximately 300 ms).

3.2.4 Motion Analysis. Participants performed the pointing task with a stylus in their right hand. An infrared-emitting diode was placed at the tip of the stylus and 3D position was monitored using an OPTOTRAK (Northern Digital, Waterloo, Ontario) motion analysis system (spatial resolution 0.01 mm). The tip of the stylus was equipped with a microswitch that provided an analog signal indicating whether or not the stylus was in contact with the surface of the display. The 3D position of the stylus and the status of the microswitch were sampled at 500 Hz. Raw data from the OPTOTRAK were converted into 3D coordinates and digitally filtered using a second order dual-pass Butterworth filter with a low-pass cutoff frequency of 10 Hz. The start and end of the movement were determined by the status of the stylus microswitch.

3.2.5 Procedure and Design. In an initial session, participants completed two practice blocks of 40 trials in which they made a pointing movement from the home position to the

center square target with a movement time goal of 240 to 360 ms. At the start of each trial the target boxes would appear and participants were instructed that this was the cue to initiate their movement. Participants were to react as quickly as possible to the onset of the boxes and complete their movement to the center target within the desired time-frame. Participants were provided with reaction time and movement time feedback on each practice trial. The second practice block differed from the first, in that a neutral prime-neutral mask sequence was presented in the center target box on all trials. The prime-mask sequence randomly appeared either before movement onset (28 ms after the target boxes; 20 trials), or upon movement initiation (20 trials) and cued participants to continue their point to the center target. In order to proceed with the experiment, participants were required to meet a movement time criterion in which the 40 trials of the second practice block had to have been performed with a mean movement time between 240 to 360 ms.

Upon successful completion of the second practice block, participants completed a Mask Pointing task and a Prime Identification task. The tasks were performed over two experimental sessions, with the first session performed immediately following the practice blocks. In the Mask Pointing task, participants made pointing movements with a stylus from a home position to one of the three possible targets. Similar to the practice trials, the start of each trial was indicated by the appearance of the targets. Participants were instructed to react as quickly as possible to the onset of the targets and initiate a movement to the center target box. Participants were further instructed that movements should be completed within 240 to 360 ms. 28 ms after the targets first appeared (before movement onset) or upon stylus lift-off (movement onset), a prime-mask sequence was displayed in the center target. In contrast to the practice blocks, left, right and neutral masks were presented equally often and could be preceded by left, right or neutral primes. The directional masks (i.e. left and right arrow masks) cued participants to modify their initial movements to the center target and complete their point to the target corresponding to the identity of the mask (i.e. if the left mask was displayed, the movement was to be completed to the left target). If the neutral mask was displayed, the movement was to continue to the center target (see Figure 1). Although there were no reaction time constraints, we continued to provide reaction time feedback on every trial, as we wanted participants to initiate their movements to the center target box as quickly as possible in response to the onset of the boxes. We did not want participants to wait to

initiate their movement in hopes that a mask would appear cuing the response required. Movement time feedback was provided only on trials in which a neutral prime and mask were displayed and movement time fell outside the desired bandwidth.

Participants performed one block of 90 trials in order to complete the first testing session. Within the block of trials, the prime-mask sequence was randomly displayed before (45 trials) or at movement onset (45 trials) and all combinations of primes and masks were presented equally often. In the second testing session, participants were reacquainted with the task constraints by completing the two practice blocks performed in the first testing session. However, participants only performed 20 practice trials in each practice block, as opposed to the original 40 completed on the first testing day. Participants then completed two more blocks of 90 trials of the <u>Mask Pointing</u> task.

Finally, to complete the second testing session, participants were made aware of the presence of the primes and attempted to identify which prime had been displayed in a <u>Prime</u> <u>Identification</u> task. Participants were told that one of three prime shapes would be presented randomly on each trial, with equal probability, and their task was to identify which one had been displayed by making a 3-alternative forced choice response. They were also told that only accuracy was being measured and that response speed was no longer important. The display sequence differed slightly from the <u>Mask Pointing</u> task in that only left or right masks were displayed. However, all primes were displayed equally often. Participants viewed the prime-mask sequence with their right index finger resting below a serial response box (Psychology Software Tools, model 300). A tone sounded 400 ms following mask onset, indicating that participants could respond by pressing the left key, the center key, or the right key with their right index finger to indicate a left pointing, neutral or right pointing prime arrow, respectively. Each participant completed 120 trials.

3.3 Data Analyses and Results

3.3.1 Prelude: Practice Trials

Performance on the second practice block in the initial testing session was used as a screening procedure to ensure that participants could complete the movement in the time allotted (240 to 360 ms). Mean movement time (MT) to the center target for our eleven participants was well within the desired bandwidth ($\bar{x} = 301 \text{ ms} \pm 29 \text{ SD}$) and did not differ

on trials in which the prime-mask sequence was displayed before movement onset ($\bar{x} = 297$ ms ± 32 SD) compared to those in which it was presented at movement onset ($\bar{x} = 305$ ms ± 29 SD), F(1,10) = 2.749, p = 0.146.

In addition to using this block of trials as a screening procedure in terms of MT, the practice trials provided a measure of how quickly participants reacted to the onset of the target boxes and initiated a movement to the center target. Mean reaction time (RT) was 244 ms \pm 30 SD. In contrast to MT, RT differed between the two types of trials. RT was significantly faster on trials when the prime-mask sequence was displayed before movement onset ($\bar{x} = 235 \text{ ms} \pm 23 \text{ SD}$) compared to trials in which it was presented at movement onset ($\bar{x} = 253 \text{ ms} \pm 38 \text{ SD}$), F(1,10) = 6.432, p = 0.03.

3.3.2 Part I: Presentation of Prime-Mask Sequence before Movement Onset

<u>Errors</u>. Participants always landed in the center target on trials in which a neutral prime preceded a neutral mask (direct pointing trials). Thus, the remaining trials in which a directional prime or mask was displayed (perturbed trials), were classified as having been modified to the left or right target if endpoint positions fell outside the center target and to the left or right respectively. In Figure 2 the percentage of corrected perturbed trials in which a left or right directional mask was displayed are presented as a function of mean movement time achieved on direct pointing trials for each participant. From this figure it is evident that all participants completed their movements to the correct eccentric target on the majority of perturbed trials in which a left or right mask was presented ($\bar{x} = 92.1\% \pm 11.2$ SD, Range: 67.8% to 100%), and that direct pointing trials were completed within the desired MT bandwidth.

Of the remaining trials, 80% were incorrectly completed to the center target when a directional mask was displayed. These trials, along with trials completed to an incorrect eccentric target were considered errors and were not included in further analyses.

<u>Temporal Characteristics</u>. Participants initiated their pointing movements on average 252 ms \pm 29 SD after the onset of the target boxes. Comparing this RT to that observed on corresponding practice trials, it is evident that participants reacted to the onset of the target boxes as instructed. Specifically, RT in the <u>Mask Pointing</u> task did not differ from that

observed on practice trials in which the prime-mask sequence was displayed before movement onset (F(1,10) = 4.783, p = 0.054) and RT was similar across all prime-mask combinations in the <u>Mask Pointing</u> task (3 Mask (Left, Right or Neutral) by 3 Prime (Left, Right or Neutral) repeated measures ANOVA: Mask: F(2,20) = 0.597, p = 0.560, Prime: F(2,20) = 0.354, p = 0.706, Mask x Prime: F(4,40) = 1.746, p = 0.189). The mean RT for all prime-mask combinations are provided in Table 1.

As illustrated in Figure 2, all participants completed their movements to the center target on direct pointing trials within the desired MT bandwidth ($\bar{x} = 285 \text{ ms} \pm 30 \text{ SD}$). In addition, we found that MT fell within the desired bandwidth, regardless of the prime-mask sequence displayed ($\bar{x} = 297 \text{ ms} \pm 37 \text{ SD}$). However, some of these movement times did differ from each other. ANOVA revealed a significant main effect for mask (F(2,20) = 12.439, p < 0.001), a non-significant main effect for prime (F(2,20) = 1.711, p = 0.225), and a significant interaction (F(4,40) = 9.418, p < 0.001). Post-hoc tests (Tukey's HSD, p = 0.05) indicated that movements were slower when completed to the left target compared to the right and center target and on incongruent trials to the left target (i.e. right prime-left mask trials) compared to congruent trials (i.e. left prime-left mask trials) (mean values are provided for all prime-mask combinations in Table 1).

Spatial characteristics. In accordance with the MT results, the length of resultant trajectories in the x-y plane (i.e. 2 dimensional displacements) were influenced by the prime-mask sequence displayed. ANOVA revealed a significant main effect for mask (F(2,20) = 23.316, p < 0.001), a non-significant effect for prime (F(2,20) = 1.221, p = 0.316) and a significant interaction (F(4,40) = 8.851, p < 0.001). Post hoc analyses (Tukey's HSD, p = 0.05) indicated that movements were shortest when completed to the center target. Moreover, trajectories were significantly longer on trials completed to the left eccentric target when the prime and mask were incongruent compared to congruent trials (i.e. right prime-left mask trials versus left prime-left mask trials).

In addition to trajectory displacement data, endpoint positions achieved within the targets further revealed that movements were influenced by the prime displayed (Mask: F(2,20) = 447.394, p < 0.001, Prime: (F(2,20) = 9.453, p = 0.001), Mask x Prime: F(4,40) < 1). Specifically, post hoc analyses (Tukey's HSD, p = 0.05) indicated that movements were

completed at a position further to the left within the designated target on trials in which a left prime was displayed, compared to trials in which a right or neutral prime was presented.

Taken together the spatial and temporal results indicate that the primes had an influence on movement. This influence was very subtle, as large modifications in trajectories in the direction of the prime were not observed (see Cressman et al., 2006). Therefore, in attempt to estimate when in the trajectory the primes first began to influence movement we calculated a mean path for each prime-mask combination displayed and determined the angles of these paths from the horizontal x-axis at 5 mm intervals. Points in the mean paths were calculated for each participant for each prime-mask combination by deriving the mean lateral and vertical position in the x-y plane for every 5 mm of movement progression along the curve. If a trajectory did not have a position value at the exact spatial location required, one was obtained by linear interpolation from the closest data points.

Figure 3 provides examples of mean paths for one participant. From these path profiles we observe that trajectories immediately diverged from the starting position depending on the prime-mask sequence displayed. In fact, at just 5 mm into the movement, ANOVA revealed significant main effects for mask (F(2,20) = 4.439, p = 0.05) and prime (F(2,20) = 14.438, p < 0.001) and a non-significant interaction (F(4,40) = 2.391, p = 0.067). Although a significant main effect was obtained for mask, post hoc analyses indicated no two means were significantly different from each other. However, when a left prime was displayed, the angle of the trajectory from the horizontal ($\bar{x} = 96.8^{\circ} \pm 8.4$ SD) was significantly greater (i.e. more to the left) than when a right ($\bar{x} = 93.1^{\circ} \pm 8.2$ SD) or neutral prime ($\bar{x} = 94.4^{\circ} \pm 8.2$ SD) was presented. In accordance with the endpoint position results discussed previously, the influence of the prime continued throughout the movement (Mask: F(2,20) = 213.078, p < 0.001, Prime: F(2,20) = 14.567, p < 0.001, Mask x Prime: F(4,40) < 1), regardless of the target achieved. Movements were completed at a greater angle from the horizontal when a left prime was displayed ($\bar{x} = 90.1^{\circ} \pm 9.6$ SD) compared to a neutral ($\bar{x} = 88.7^{\circ} \pm 9.6$ SD) or a right prime ($\bar{x} = 87.2^{\circ} \pm 9.7$ SD), which differed from each other.

3.3.3 Part II: Presentation of Prime-Mask Sequence at Movement Onset Participants landed in the center target on all direct pointing trials. Thus, in a similar classification process as outlined above, perturbed trials were considered to have been

completed to the left or right target if endpoint positions fell outside the center target and to the left or right respectively. In Figure 4 the percentage of corrected perturbed trials in which a left or right directional mask was displayed are presented as a function of mean movement time achieved on direct pointing trials for each participant. From this figure we can observe that, as a whole, participants were not as successful at completing their movements to the appropriate target on these trials compared to when the prime-mask sequence was presented before movement onset. Furthermore, the speed at which participants were moving appears to have determined the percentage of trials they were able to correctly modify.

Due to the range in performance we divided participants into two groups (Responders and Non-Responders). Participants S11, S08, S10 and S09 modified their movements on the majority of trials and were classified as Responders. They were also the participants who completed their movements to the center target on direct pointing trials in the longest MT. Participants S02, S07, S01, S05 and S04 were classified as Non-Responders. They achieved the fastest MT on direct pointing trials and were unable to modify their movements to the correct eccentric target (i.e. completed their movements to the center target on the majority of trials). We decided to group the two remaining participants (S03 and S06) with the Responders because even though their MT on direct pointing trials lay between the two groups, they correctly modified their movements on more than double the number of trials of any participant in the Non-Responder Group.

As discussed above, the Responders were slower to complete their movements to the center target compared to the Non-Responders. In fact, mean MT to the center target on direct pointing trials for the Responders ($\bar{x} = 362 \text{ ms} \pm 32 \text{ SD}$) lay just outside the MT bandwidth and was significantly greater than MT achieved by the Non-Responders ($\bar{x} = 294 \text{ ms} \pm 16 \text{ SD}$), Welch t' test: t(8) = 4.5, p < 0.03. From these results it is questionable if performance of the Responders can be examined in light of dorsal stream processing (Pisella et al., 2000). In attempt to resolve this issue, we compared the initial phases of direct pointing trials between the two groups and found that even though movements were completed with differing latencies, all participants appeared to plan and initiate similar movements. Specifically, Welch t' tests revealed that peak velocity achieved within the first 100 ms (t(8) = 0.939, p > 0.05), time of peak velocity (t(9) = 0.017, p > 0.05), peak acceleration achieved within the first 100 ms (t(8) = 0.799, p = > 0.05) and time of peak

acceleration (t(9) = 0.43, p > 0.05) on direct pointing trials did not differ between the two groups. Furthermore, it is important to remember that the Responders completed movements to the center target on direct pointing trials when the prime-mask sequence was displayed before movement onset within the time allotted ($\bar{x} = 303 \text{ ms} \pm 30 \text{ SD}$). Trials in which the prime-mask sequence was presented before movement onset were randomly intermixed with trials in which the stimuli were displayed at movement onset. Thus it is assumed that all participants planned similar 300 ms movements on all trials and at least the initial phases of the movements were under dorsal stream control.

3.3.3.1 Movement characteristics of the Responders

Errors. The six Responders correctly completed their movements on perturbed trials 69.3% ± 17.4 SD of the time. Of the remaining perturbed trials, $21.8\% \pm 16.4$ SD were incorrectly completed to the eccentric target specified by the prime. Although trials completed to the target specified by the prime could be considered evidence of the impact of the prime on movement, these trials were excluded from analyses due to their limited number. In addition, movements completed to the center target when a directional mask was presented were considered errors and excluded from further analyses. Hence, the results discussed below pertain only to performance on perturbed trials in which movements were completed to the correct target.

In order to examine the potential influence of the primes on movement, we compared individual perturbed trials to a mean path calculated for each participant from all direct pointing trials. The points in the mean paths were calculated by deriving the mean lateral and vertical position in the x-y plane for every 5 mm of movement progression along the curve. In addition, the standard deviation of the mean position in the x-direction was also determined at corresponding 5 mm intervals. The resulting mean spatial trajectory, together with its 2 standard deviation bandwidth, then became the standard against which pointing on perturbed trials were assessed. As can be observed in Figure 5, in contrast to the profiles displayed in Figure 3, trajectories were initiated to the center target and then modified in the direction of the prime when the prime-mask sequence was presented at movement onset.

The trials in which a directional prime preceded a neutral mask proved difficult to analyze. On some of these trials, a movement was completed within the 2 standard deviation

bandwidth of the direct pointing trials and thus, it was not evident if a directional prime had had an influence on the trajectory or not. Therefore, in order for these trials to have been considered modified, a trajectory had to first cross the 2 standard deviation bandwidth of the direct pointing trials in the direction of the prime and then be reversed such that the movement was completed towards the center target. Based on these criteria, 42.6% of all directional prime-neutral mask trials were classified as having been modified. Because these trials reflect the trajectories in which the primes had the greatest influence on movement, data corresponding to these trials are only provided for the purpose of comparison and are not included in statistical analyses. In order to account for the exclusion of these trials from statistical analysis, a 2 Mask (Left or Right) by 3 prime congruency (Congruent, Incongruent or Neutral with respect to the mask) repeated measures analysis of variance (ANOVA) was used to analyze performance measures obtained on the remaining perturbed trials.

<u>Temporal Characteristics</u>. Participants initiated their pointing movements 265 ms ± 44 SD after the appearance of the target boxes on direct pointing trials. This RT did not differ from the RT observed for the same participants on practice trials in which the prime-mask sequence was displayed at movement onset (F(1,5) = 1.749, p = 0.243). Furthermore, there were no differences in RT between any of the movements completed to the left or right eccentric target in the <u>Mask Pointing</u> trials, providing additional evidence that participants reacted to the onset of the target boxes as instructed (Mask: F(1,5) = 0.09, p = 0.776, Prime: F(2,10) = 2.185, p = 0.163, Mask by Prime Congruency: F(2,10) = 1.165, p = 0.351). Mean values are provided for all prime-mask combinations in Table 2a.

MT on direct pointing trials ($\bar{x} = 362 \text{ ms} \pm 32 \text{ SD}$) was significantly greater than that observed on practice trials for the same participants ($\bar{x} = 304 \text{ ms} \pm 29 \text{ SD}$), F(1,5) = 18.329, p = 0.008), but significantly shorter than perturbed pointing trials completed to an eccentric target (F(1, 5) = 81.09, p < 0.001). To examine the influence of a prime on MT to the eccentric targets we performed a 2 Mask by 3 Prime Congruency repeated measures ANOVA. ANOVA revealed significant main effects for mask (F(1,5) = 9.739, p = 0.026) and prime (F(2,10) = 20.337, p < 0.001) and a non-significant interaction (F(2,10) = 1.89, p= 0.201. Movements were completed faster to the right target than to the left target and on trials in which the prime and mask were congruent ($\bar{x} = 451 \text{ ms} \pm 24 \text{ SD}$) compared to

incongruent ($\overline{x} = 560 \text{ ms} \pm 26 \text{ SD}$) and neutral prime trials ($\overline{x} = 533 \text{ ms} \pm 53 \text{ SD}$). Incongruent and neutral prime-mask trials did not differ from each other (Tukey's HSD, p = 0.05). On trials in which a directional prime preceded a neutral mask and the trajectory was modified in the direction of the prime, MT was on average $566 \pm 32 \text{ ms}$.

From the MT results and trajectories observed in Figure 5 it is evident that the primes had an impact on movement, however, what is not yet clear is when this influence arose. In order to address this issue a conservative estimate of the time at which the movement began to deviate toward the target specified by the mask was calculated. This estimate was defined as the point in time at which displacement in the horizontal axis of the movement achieved a maximal value and showed a reversal toward the appropriate target. The time at which the movement began to deviate toward the target specified by the mask was dependent upon prime congruency (F(2,10) = 37.649, p = 0.001). Tukey's HSD (p = 0.05) analyses revealed that movements were corrected to the appropriate target at a significantly shorter latency on trials in which the prime and mask were congruent ($\bar{x} = 239 \text{ ms} \pm 10 \text{ SD}$) compared to incongruent trials ($\bar{x} = 338 \text{ ms} \pm 14 \text{ SD}$) and neutral trials ($\bar{x} = 296 \text{ ms} \pm 31 \text{ SD}$), which did not differ from each other. This effect was independent of the mask displayed (Mask: (F(1,5) < 1, Mask by Prime Congruency: F(2,10) < 1). In the directional prime-neutral mask trials modifications were observed at a latency of 395 ms $\pm 29 \text{ SD}$.

<u>Spatial Characteristics</u>. Based on the trials displayed in Figure 5, it is evident that trajectories were first modified in the direction of the prime. Thus, on incongruent trials, participants had to correct for these initial modifications in order to complete the movement to the correct target. In order to quantify this observation we measured the horizontal distance from the point in time at which a trajectory showed a reversal to the correct target to the center of the corresponding eccentric target. ANOVA revealed a non-significant main effect for mask (F(1,5) = 1.755, p = 0.243), a significant main effect for prime congruency (F(2,10) = 11.099, p < 0.018) and a non-significant interaction (F(2,10) < 1). Although post hoc analyses failed to locate a difference in horizontal distance (Tukey's HSD, p = 0.05), data suggest that participants had greater modifications in movement trajectories when the prime and mask were incongruent ($\bar{x} = 94.9 \text{ mm} \pm 16.1 \text{ SD}$) compared to congruent ($\bar{x} = 71.9 \text{ mm}$

 \pm 2.9 SD) and neutral prime trials ($\bar{x} = 73.7 \text{ mm} \pm 4.7 \text{ SD}$). On directional prime-neutral mask trials, movements were modified 43.5 mm \pm 10.1 SD in the direction of the prime before being reversed to the center target.

Perturbed trials in which a Neutral Mask was displayed. In the results discussed above, perturbed trials in which a neutral mask was displayed were considered to have been modified only if a trajectory crossed the 2 standard deviation bandwidth of the mean path in the direction of the prime before being reversed towards the center target. This requirement excluded a number of perturbed trials correctly completed to the center target from analyses. Hence, in order to illustrate that the primes did have an overall influence on these movements and in attempt to obtain an index of when this influence arose, we computed mean paths for left prime-neutral mask trials and right prime-neutral mask trials for each participant. Figure 6 presents examples of mean paths computed for a typical participant. Similar to the individual profiles displayed in Figure 5, the mean paths presented in Figure 6 illustrate that participants initiated their movements to the center target as instructed and these movements were first modified in the direction of the prime.

In attempt to identify the point in time at which the primes had an influence on movement in these trials, we examined when the mean profiles diverged from each other. Specifically, we determined the distance participants had traveled in the forward y-direction when the horizontal distance between the left prime-neutral mask mean path and the right prime-neutral mask mean path first exceeded 5 mm for each participant (Note: the mean standard deviation achieved in the horizontal direction of the direct pointing trials was $\bar{x} = 6.27 \text{ mm} \pm 1.6 \text{ SD}$). We then went back to the individual profiles and established the time corresponding to when this distance had been achieved, regardless of whether or not the trial met the criteria for having been modified. Based on this analysis we found that the mean paths diverged at approximately 222 ms $\pm 60 \text{ SD}$. This latency corresponds to when the primes first had an impact on trajectories in these trials and is of a similar magnitude to when we first observed modifications in trajectories from the center target to the correct eccentric target on congruent trials (239 ms). Given that these deviations are of a similar latency when the same directional primes were displayed, we are confident that the modifications observed

in congruent trials arose from prime processing and are reflective of the time at which the prime first had an impact on movement.

3.3.3.2 Movement characteristics of the Non-Responders

<u>Errors</u>. The remaining 5 participants completed their movements to the center target $83.8\% \pm 3.0$ SD of the time and on $81.5\% \pm 3.0$ SD (Range: 73.3% to 89.3%) of the trials in which a directional left or right mask was displayed. Of the remaining perturbed trials, $69.9\% \pm 20.4$ SD were completed to the correct eccentric target. Due to the limited number of correct responses to an eccentric target, only trials in which movements were completed to the center target were included in analyses.

<u>Temporal Characteristics</u>. Mean RT for this group of participants was 299 ms \pm 15 SD on direct pointing trials, which did not differ from the RT observed for the same participants on practice trials in which the prime-mask sequence was displayed at movement onset (F(1,4) = 6.507, p = 0.063). In terms of the <u>Mask Pointing</u> trials, a 3 Mask (Left, Right or Neutral) by 3 Prime (Left, Right or Neutral) repeated measures ANOVA revealed a significant main effect for mask (F(2,8) = 4.682, p = 0.045, a non-significant effect for prime (F(2,8) < 1) and a non-significant interaction (F(4,16) = 1.327, p = 0.302). RT was significantly greater on trials in which a neutral mask was presented compared to when a right mask was displayed (Tukey's HSD, p = 0.05). Mean values are provided for all prime-mask combinations in Table 2b.

MT on direct pointing trials ($\bar{x} = 294 \text{ ms} \pm 16 \text{ SD}$) was within the goal movement time bandwidth and did not differ from MT achieved on practice trials for the same participants ($\bar{x} = 305 \text{ ms} \pm 34 \text{ SD}$; F(1,4) = 0.506, p = 0.516). In contrast to the Responders, MT for all trials was within the desired bandwidth ($\bar{x} = 285 \text{ ms} \pm 21 \text{ SD}$) and ANOVA revealed non-significant main effects (Mask: F(2,8) = 3.301, p = 0.09, Prime: F(2,8) = 0.656, p = 0.545) and a significant interaction (F(4,16) = 3.76, p = 0.024). Tukey's HSD (p = 0.05) indicated that differences in MT arose between trials in which a neutral prime preceded a left mask compared to trials in which a left prime-left mask sequence was displayed.

<u>Spatial Characteristics</u>. The temporal results, in addition to the fact that movements were completed to the center target, suggest that the identity of the prime had a limited impact on movement. This was confirmed by analyzing endpoint position. Although, endpoint position within the center target was further to the left when a left prime was displayed ($\bar{x} = -2.3 \text{ mm} \pm 3.4 \text{ SD}$ left of center), compared to a neutral prime ($\bar{x} = -0.2 \text{ mm} \pm 4.2 \text{ SD}$ left of center) and a right prime ($\bar{x} = 1.9 \text{ mm} \pm 6.5 \text{ SD}$ right of center), these findings failed to reach significance (mask: F(2,8) < 1, prime: F(2,8) = 2.803, p = 0.167, mask by prime: F(4,16) < 1).

3.3.4 Perceptual Awareness

Participants were surprised to learn that mask arrows had been preceded by prime arrows and indicated they were merely guessing in the <u>Prime Identification</u> task. These subjective reports were supported by participants' inability to correctly discriminate between the primes in the <u>Prime Identification</u> task ($\bar{x} = 50.2\% \pm 13.3$ SD). A chi-square goodnessof-fit task revealed that perceptual performance did not differ significantly from the chance level of 33% (p > 0.05).

3.4 Discussion

The goal of the present experiment was to determine if the influence of a subliminal prime stimulus on action can be mediated by the dorsal stream. In order to address this issue, we examined the influence of prime stimuli on rapid, visually guided actions whose characteristics were particularly suited for dorsal stream control. Participants were instructed to complete a goal-directed movement to a center target within 300 ms. If a directional mask arrow appeared, participants were to attempt to modify this initial movement and complete their point to the corresponding eccentric target. The critical prime-mask sequence was randomly presented either within the reaction time interval or upon movement onset.

Using a similar paradigm, we have recently demonstrated that when reaching trajectories are completed with a movement time goal of 400+ ms and the prime-mask sequence is presented at movement onset, movements deviate in the direction cued by the prime (see Cressman et al., 2006). However, while these results show that prime related

visuomotor processing can take over the control of a goal-directed movement, they do not indicate if this unconscious control arises due to visuomotor processing occurring in the dorsal stream (e.g. given the long latency of these responses, it may have been possible for operations occurring within the ventral stream to gain access to movement control; see Pisella et al., 2000). Thus, in order to examine the possible influence of prime stimuli on action in the current investigation in light of dorsal stream processing, we had participants complete their trajectories in a time-frame in which any adjustments in trajectory in the direction of the prime would be a signature of the operation of the dorsal stream.

Participants planned and initiated movements to the center target. On the majority of trials completed to the center target, movement times were within the goal time (approximately 300 ms). On trials in which the prime-mask sequence was presented at movement onset, participants' initial trajectories were in the direction of the center target. Half of the participants (the Responders), then modified these initial trajectories in response to the prime at a latency of approximately 240 ms. The remaining participants (the Non-responders) were unable to correct their trajectories and completed their movements to the center target on the majority of trials in a movement time of 285 ms. Despite the fact that the Non-Responders completed their movements to the center target, results suggest that the primes did begin to have an influence on movement. For example, end point positions within the center target displayed a slight bias in the direction of the prime. In addition, there was a small portion of trials (< 7% overall) that were completed to the eccentric targets designated by the primes within the goal movement time. Therefore, taken together these results imply that fast, rapid movements mediated by the dorsal stream, can be modified on-line in response to subliminal stimuli.

In order to determine if similar stream processes were engaged during the reaction time interval we included trials in which the prime-mask sequence was presented before movement onset. On these trials, we found that all participants achieved the correct target on the majority of trials within the movement time goal. More importantly, however, was the finding that movements were initiated in the direction of the prime. The mean reaction time of these trials was 255 ms and because the prime-mask sequence was not displayed until 28 ms into the reaction time interval, the influence of the prime was first observed at an approximate latency of 230 ms. This latency is of a similar magnitude to that obtained when

the prime-mask sequence was presented at movement onset and trajectories were modified on-line in response to the prime. Furthermore, the influence of the primes on action continued throughout the movements, such that endpoint positions within the designated target were biased by the prime displayed (i.e. movements within a given target were completed more to the left when a left prime was presented compared to a neutral prime).

Combining the results across all trials (i.e. trials in which the prime-mask sequence was presented within the reaction time interval and at movement onset), it is evident that the primes took over control of a goal-directed movement. Moreover, given the similarity of the time at which this influence arose (~240 ms), it appears that similar processes were engaged, regardless of the time of prime presentation. Based on these findings and given the task constraints, we propose that the influence of the primes on action arose automatically, due to processes occurring within the dorsal visual stream. Thus, in addition to revealing that the influence of a prime on action can be mediated by the dorsal stream, our results extend Westwood and Goodale's (2003) proposal that dorsal stream processes are engaged once a movement is cued. Specifically, our results indicate that similar dorsal stream processes are engaged for movement modification, regardless of whether or not the limb is in flight.

While the results of the current investigation reveal that the unconscious visuomotor processing of prime stimuli can be mediated by the dorsal stream, they do not imply that the influence of masked primes on reaction time (RT) observed in previous metacontrast masking paradigms is due to similar processes. The present task employed a task whose characteristics were particularly suited for dorsal stream control. For example, participants were to modify a goal-directed movement in response to a stimulus, as opposed to initiate a response based on the identity of a stimulus. Adjustments in this goal directed movement occurred early, much earlier than RT observed in previous metacontrast masking RT paradigms (e.g. see Ansorge et al., 2002; Vorberg et al., 2003; Cressman et al., 2006). In addition the current investigation differed from typical metacontrast masking RT paradigms employed in terms of the number of effectors involved and the ability of participants to modify their initial responses. In the present task, participants used only one limb to respond and the movement was continuous, such that initial errors could be corrected on-line. In contrast, typical metacontrast masking RT paradigms require participants to make a discrete response by pressing a left or right key with the left or right index finger, respectively.

The relationship between these variables (i.e. (1) movement phase: response execution versus response initiation, (2) number of effectors: 1 versus 2 and (3) nature of the task: continuous versus discrete) and the possible role they play in dictating the different visual processes involved in prime processing still needs to be resolved. However, recent work by Schmidt (2002) and Adam and Pratt (2004) begins to address some of these issues. Specifically, results reveal that it may not be the movement phase completed that controls the visual processes engaged but rather the number of effectors involved or the nature of the task itself. For example, Schmidt (2002) recently demonstrated that a prime can take over control of a movement, even under circumstances in which the task is one of response initiation. Schmidt (2002) adapted classic metacontrast masking procedures and had his participants make short aiming movements as opposed to key press responses. The display consisted of isoluminant red and green disks (primes) presented simultaneously in diagonally opposite quadrants of a screen, 32 mm away from a central fixation point. The primes were displayed for 10 ms and masked by red and green annuli that appeared 0 to 50 ms after prime offset. Participants were instructed to point as quickly and accurately as possible from the central fixation point to an annulus with a pre-specified colour (e.g. red). Similar to the results obtained in the present experiment, Schmidt found that initial responses were strongly influenced by the presence and location of the red prime. Specifically, participants initiated their movements approximately 230 ms after prime onset, in the direction of the prime. Based on these results, it would appear that the dorsal stream is capable of processing such attributes as colour and the orientation of a prime stimulus for the control of action, regardless of whether the action is to be initiated or modified on-line in response to a target mask stimulus (see also Appendix A).

It is important to note that in both Schmidt's (2002) task and the experimental paradigm we employed in the present investigation, participants completed their responses with one limb and were able to correct their initial movements. Thus, perhaps the longer latency in response times obtained in typical metacontrast masking RT tasks arises due to participants having to select a response limb or wanting to ensure that they initiate the correct response. This added time may allow processes occurring in the ventral stream to gain access to action. Hence explaining why RT benefits are observed in metacontrast masking

RT tasks, regardless of the nature of the stimuli (i.e. shape, orientation, colour, or semantics), and why responses are initiated in accordance with the mask as opposed to the prime.

In support of the notion that additional processes may be required when limb selection is involved in the response process, Adam and Pratt (2004) have recently demonstrated performance differences in a RT precue task depending on the number of effectors in the response set. In their task, participants were instructed to (1) press a key corresponding to the location of a target light or (2) move their index finger to the target light. There were four possible target locations, which corresponded to 4 response keys in the RT task (index and middle fingers of the left and right hand were used to make responses in the key press task and the right index finger was used to make all responses in the pointing task). On each trial, a precue preceded the target and indicated possible target locations. In addition to finding that RT was faster in the pointing task overall, results indicated that differences in the influence of the precues on performance (i.e. amount and pattern of precuing effects) arose depending on the task completed (key press or pointing). Based on these results, Adam and Pratt (2004) concluded that single-effector (i.e. pointing) and multiple-effector (i.e. key press) tasks are controlled by different mechanisms.

The notion that limb selection (or possibly the nature of the movement to be completed) may increase response time, thus allowing time for processes occurring in the ventral stream to influence behaviour, is put forth as a hypothesis. Additional work is clearly required before the nature of subliminal prime processing for the control of action can be understood in any great detail. At present, we suggest that it is possible for processing within the dorsal stream to give rise to the influence of a prime on action, when certain task restrictions are met.

3.5 Bridging Summary

From the results obtained in Studies 1 and 2 it is evident that invisible primes can automatically take over control of a goal-directed action. However, by comparing these results to those obtained in typical metacontrast masking RT paradigms (see Study 1: Mask Response Time task) it appears that the impact of subliminal stimuli on action is dependent on task constraints. For example, in RT paradigms, participants' first recorded responses are almost always consistent with the identity of the mask (i.e. participants appear to wait until they *identify* the mask before committing to an overt response). In contrast, when the primemask sequence is presented during the execution of a goal-directed movement, participants first respond in the direction of the prime. Thus, these findings suggest that while the impact of subliminal events on action may be automatic within a particular task (i.e. a prime automatically influences action in a pointing task), unconscious visuomotor processes do not evoke a set response between tasks, as put forth by top-down contingency accounts of subliminal processing. Instead, the ability of subliminal stimuli to influence motor behaviour is modulated depending on task constraints.

In the current experiment we continued our investigation into "*automatic*" subliminal visuomotor guidance. Specifically, we were interested in determining whether unconscious processes could be modulated by changing the task relevance of a particular stimulus. Participants were instructed to make the same goal-directed movement as in Study 1 and to modify the movement if a directional arrow mask was presented. In contrast to Study 1, participants were warned that a particular directional arrow would be displayed on the majority of trials. According to top-down contingency accounts, the influence of subliminal stimuli on action is guided by one's intentions. Thus, we hypothesized that the ability of a prime to take over the control of a goal-directed movement would be dependent on its relationship to the more probable directional mask (i.e. a prime pointing in the same direction as the high probability mask would have a different influence on performance than a prime pointing in the opposite direction).

3.6 Tables

Table 3.1. Mean (SD) performance for movements in which the prime-mask sequence was displayed before movement onset and movements were completed to the correct target.

Mask	Left			Right			Neutral		
Prime	Left	Right	Neutral	Left	Right	Neutral	Left	Right	Neutral
RT	254 (24)	251 (22)	256 (35)	259 (38)	251 (33)	248 (30)	244 (28)	249 (25)	255 (30)
MT	307 (40)	328 (31)	312 (39)	285 (48)	279 (47)	295 (46)	290 (30)	292 (40)	285 (31)
2DD	273 (16)	283 (15)	278 (17)	276 (14)	271 (12)	275 (15)	259 (8)	259 (9)	255 (7)
End	-68.1 (11.9)	-64.6 (12.4)	-66.7 (12.1)	58.6 (10.5)	64.5 (8.3)	63.0 (9.3)	-2.8 (4.4)	0.88 (4.8)	-0.53 (2.7)
A-5mm	97.9 (9.5)	94.1 (8.4)	97.1 (7.8)	93.3 (8.1)	92.5 (8.5)	91.4 (7.6)	97.2 (8.2)	92.6 (8.4)	94.6 (8.8)
A-end	101.1 (3.4)	98.5 (3.1)	99.8 (3.5)	78.9 (2.9)	76.0 (2.2)	77.5 (2.5)	90.2 (1.5)	87.2 (2.0)	88.6 (0.8)

RT: Reaction time (ms), MT: Movement time (ms), 2DD: 2 dimensional displacement along the curve (mm), End: Position of touch down with respect to the middle of the center target (mm), A-5mm: Angle of the trajectory from the horizontal axis at 5 mm into the movement, A-end: Angle of the trajectory from the horizontal axis at the end of the movement.

Table 3.2a. Mean (SD) performance of the Responders on trials in which the prime-mask sequence was displayed at movement onset and movements were completed to the correct target.

Mask	Left			Right			Neutral			
Prime	Left	Right	Neutral	Left	Right	Neutral	Left	Right	Neutral	
RT	274 (62)	280 (35)	261 (54)	273 (47)	291 (73)	259 (52)	277 (43)	257 (46)	265 (45)	
MT	472 (28)	583 (29)	541 (42)	536 (36)	430 (28)	525 (68)	550 (46)	581 (50)	362 (32)	
СТ	237 (18)	335 (16)	287 (23)	341 (19)	240 (16)	304 (48)	394 (31)	397 (40)		
HD	77 (9)	98 (21)	77 (8)	92 (18)	67 (9)	71 (10)	41 (9)	46 (14)		

Mask	Left			Right			Neutral		
Prime	Left	Right	Neutral	Left	Right	Neutral	Left	Right	Neutral
RT	270 (26)	297 (35)	271 (32)	263 (36)	268 (40)	299 (39)	293 (57)	299 (31)	299 (15)
MT	272 (18)	280 (25)	298 (17)	283 (25)	278 (26)	278 (10)	285 (23)	301 (26)	294 (16)
End	-2.2 (4.3)	1.9 (7.0)	-1.0 (2.8)	-2.7(3.3)	2.3 (7.1)	0.3 (3.4)	-2.1 (3.1)	1.5 (7.0)	0.3 (4.8)

Table 3.2b. Mean (SD) performance of the Non-Responders on trials in which the prime-mask sequence was displayed at movement onset and movements were completed to the center target.

RT: Reaction time (ms), MT: Movement time (ms), CT: Time of final trajectory modification, HD: Horizontal displacement from time of final trajectory modification to end of movement, End: Position of touch down with respect to the middle of the center target (mm).

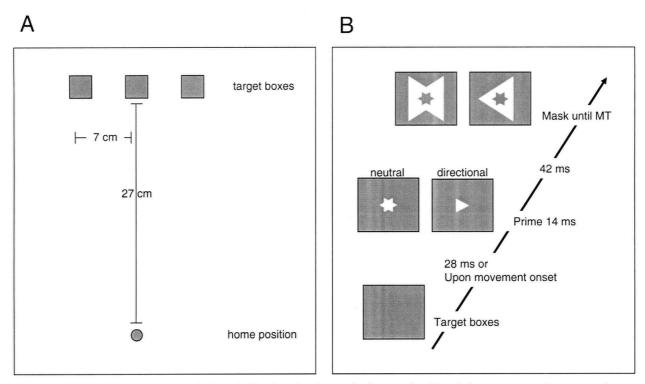
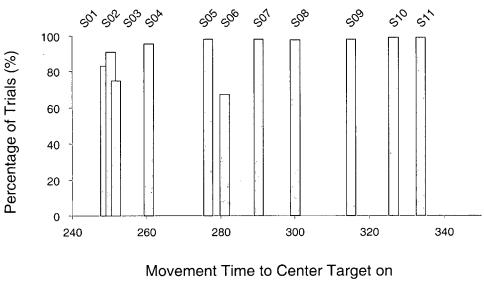
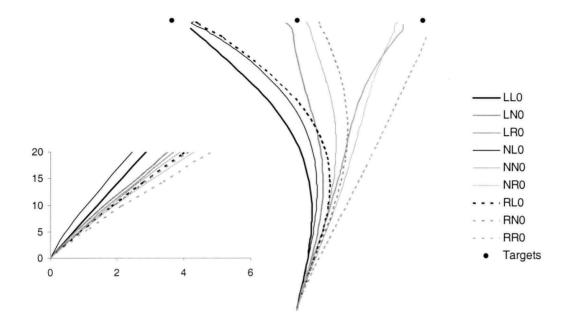


Figure 3.1. (A) Overview of visual display in the pointing task. Participants were instructed to react as quickly as possible to the onset of the target boxes and make a pointing movement from the home position to the center target box with a movement time goal of 240-360 ms. Directional arrows cued participants to modify their movements to the center target and land in an either a left or right eccentric target. (B) Temporal sequence of a direct pointing trial (left) and a perturbed pointing trial (right). Left, right and neutral masks were presented equally often and could be preceded by left, right or neutral primes. The prime-mask sequence was displayed either before movement onset (i.e. within the reaction time interval) or upon movement onset.

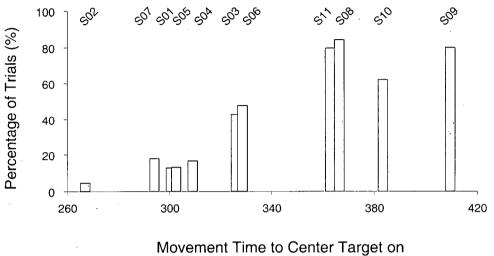


Unperturbed Trials (ms)

Figure 3.2. The percentage of corrected perturbed trials in which a left or right directional mask was displayed before movement onset as a function of mean movement time achieved on corresponding direct pointing trials for each participant (S01-S11).



<u>Figure 3.3</u>. Examples of mean paths for one participant when the prime-mask sequence was displayed before movement onset. The thicker lines correspond to when a left prime was presented, thin lines to when a neutral prime was presented and a dashed line to when a right prime was presented. Black lines indicate trials in which a left mask followed a prime, grey lines correspond to when a neutral mask was displayed and the lightest line indicates trials in which a right mask was displayed. The insert depicts the relationship between the different prime-mask combinations at the onset of movement. Note: movements were initiated in the direction corresponding to the prime displayed.



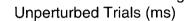


Figure 3.4. The percentage of corrected perturbed trials in which a left or right directional mask was displayed at movement onset as a function of mean movement time achieved on corresponding direct pointing trials for each participant (S01 to S11). Note the range in participants' performance.

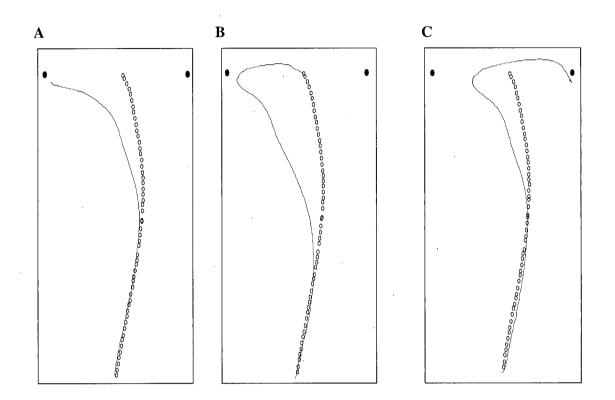
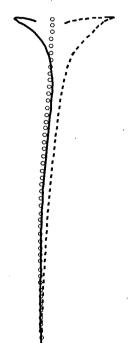


Figure 3.5. Examples of mean direct spatial trajectories (open circles) and individual perturbed spatial trajectories (solid line) under each of the three conditions in which a left prime was displayed ((A) left mask (congruent trial), (B) neutral mask and (C) right mask (incongruent trial)). The center of the eccentric target boxes are indicated by annuli (the center target box is not visible). Note the early trajectory deviation to the left eccentric target in all examples.



Prime-Mask sequence displayed

Neutral Prime-Neutral Mask
 Left Prime-Neutral Mask

- - Right Prime-Neutral Mask

Figure 3.6. Examples of mean spatial trajectories on trials in which a neutral mask was displayed. The open circles correspond to a mean path computed from direct pointing trials (neutral prime-neutral mask), the solid line to perturbed trials in which a left prime was presented and the dashed line to perturbed trials in which a right prime was presented.

3.8 References

- Adam, J.J., & Pratt, J. (2004). Dissociating visual attention and effector selection in spatial precuing tasks. *Journal of Experimental Psychology: Human Perception* and Performance, 30, 1092-1106.
- Ansorge, U., Klotz, W., & Neumann, O. (1998). Manual and verbal responses to completely masked (unreportable) stimuli: Exploring some conditions for the metacontrast dissociation. *Perception*, 27, 1177-1189.
- Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-543.
- Bard C, Turrell Y, Fleury M, Teasdale N, Lamarre Y, Martin O (1999). Deafferentation and pointing with visual double-step perturbations. *Experimental Brain Research*, 125, 410-416.
- Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.
- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1593.
- Breitmeyer, B.B., Ro, T., & Singhal, N.S. (2004). Unconscious colour priming occurs at stimulus- not percept- dependent levels of processing. *Psychological Science*, 15, 198-202.
- Brenner, E., & Smeets, J.B.B. (2004). Colour vision can contribute to fast corrections of arm movements. *Experimental Brain Research*, 158, 302-307.
- Carey, D.P., Harvey, M., & Milner, A.D. (1996). Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia*, 34, 329-337.
- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006). On-Line Control of Pointing is Modified by Unseen Visual Shapes. *Consciousness and Cognition*, in press.
- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006b). No automatic pilot for visually guided aiming based on colour. *Experimental Brain Research*, 171, 174-183.

Dehaene, S., Naccache, L, Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz,

G., van de Moortele, P-M., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597-600.

Desmurget M, & Prablanc C (1997). Postural control of three-dimensional prehension movements. *Journal of Neurophysiology*, 77, 452-464.

- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E., & Grafton, S.T. (1999). Role of the posterior cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2: 563-567.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation:
 Behavioural and Electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1737-1747.
- Enns, J.T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, 15, 20-23.
- Goodale, M.A., & Milner, A.D. (2004). Sight unseen: An exploration of conscious and unconscious vision. Oxford, UK: Oxford University Press.
- Goodale, M.A., & Westwood, D.A. (2004). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, 14, 203-211.
- Jaskowski, P., Skalska, B., & Verleger, R. (2003). How the self controls its "Automatic Pilot" when processing subliminal information. *Journal of Cognitive Neuroscience*, 15, 911-920.
- Kahneman, D. (1968). Methods, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70, 404-423.
- Klotz, W., & Neumann, O. (1999). Motor activation without conscious discrimination in metacontrast masking. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 976-992.
- Kunde, W., Kiesel, A., & Hoffmann, J. (2003). Conscious control over the content of conscious cognition. *Cognition*, 88, 223-242.
- Milner, A.D., & Goodale, M.A. (1995). The visual brain in action. Oxford, UK: Oxford University Press.
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-213.

- Neumann, O., & Klotz, w. (1994). Motor responses to nonreportable, masked stimuli:
 Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Pisella, L., Gréa, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729-736.
- Paulignan Y, MacKenzie C, Marteniuk R, & Jeannerod M (1991). Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Experimental Brain Research*, 83, 502-512.
- Pisella, L., & Rossetti, Y. (2000). Interaction between conscious identification and Non-Conscious Sensori-Motor Processing. In Y. Rossetti & A. Revonsuo (Eds.), Beyond dissociation: interaction between dissociated implicit and explicit processing (pp. 129-152). Amsterdam: John Benjamins Publishing.
- Rossetti, Y., Pisella, L., & Pélisson, D. (2000). Eye blindness and hand sight : Temporal aspects of visuomotor processing. *Visual Cognition*, 6, 785-809.
- Schmidt, T. (2002). The finger in flight: Real-time motor control by visually masked colour stimuli. *Psychological Science*, 13, 112-118.
- Schmidt, T., Niehaus, S., & Nagel, A. (2006). Primes and targets in rapid chase: Tracing sequential waves of motor activation. *Behavioural Neuroscience*, 120, 1005-1016.
- Taylor, J.L., & McCloskey, D.I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology*, 63, 439-443.
- Taylor, J.L., & McCloskey, D.I. (1996). Selection of motor responses on the basis of unperceived stimuli. *Experimental Brain Research*, 110, 62-66.
- Toth, L.J., & Assad, A. (20020. Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature*, 415, 165-168.
- Van Essen, D.C., Anderson, C.H., & Felleman, D.J. (1992). Information processing in the primate visual system: An integrated systems perspective. *Science*, 255, 419-423.
- Vath, N., & Schmidt, T. (2007). Tracing sequential waves of rapid visuomotor activation in lateralized readiness potentials. *Neuroscience*, 145, 197-208.

Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 6275-6280.

White, B.J., Kerzel, D., & Gegenfurtner, K.R. (2006). Visually guided movements to color targets. *Experimental Brain Research*, 175, 110-126.

CHAPTER 4

STUDY 3: Unconscious but under control: Subliminal behaviour is sensitive to observer expectations⁶

4.1 Introduction

Investigations into unconscious visuomotor processing have demonstrated that stimuli presented below the threshold of conscious awareness can influence motor behaviour. For example, reaction time (RT) to a visible stimulus in a two-choice RT task has been shown to be affected by a subliminal prime stimulus (Neumann and Klotz, 1994; Dehaene et al., 1998; Ansorge et al., 2002; Schmidt, 2002; Vorberg et al., 2003). In these choice RT tasks, the prime precedes the target (mask) stimulus and is rendered "invisible" to the conscious system as a result of metacontrast masking; a form of backward masking in which a briefly displayed prime stimulus is followed by a mask stimulus that closely fits the outer contours of the prime but does not touch it (for reviews of metacontrast masking see Kahneman, 1968; Breitmeyer, 1984; Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000). However, even though participants cannot detect the presence of the prime or discriminate between the primes as a result of metacontrast masking, both simple and choice response times to the mask are facilitated when it is preceded by a prime that shares attributes critical to the correct response (congruent trial) compared to a neutral stimulus. Furthermore, if the mask is preceded by a prime that shares attributes critical to the alternative response (incongruent trial), response times to the mask are slower compared to the same neutral stimulus (Taylor and McCloskey, 1990, 1996; Klotz and Neumann, 1999; Ansorge et al., 2002; Cressman et al., 2006).

It is currently unclear how these prime stimuli influence action in the absence of conscious awareness. According to the theory of Direct Parameter Specification (DPS: Neumann, 1990) and the Action Trigger Hypothesis (Kunde et al., 2003), subliminal prime stimuli are processed in a "*conditionally automatic*" manner. Specifically, the ability of a subliminal stimulus to impact action is dependent upon the existence of a prior intention to act, as only stimuli mapped to a particular response will influence performance. Moreover, according to the theory of Direct Parameter Specification and the Action Trigger Hypothesis, processes associated with the subliminal stimulus are restricted to comparing the incoming

⁶ A version of this chapter will be submitted for publication.

stimulus to an established set of stimulus-response alternatives and then, if a match is obtained, directly activating the related response (Neumann, 1990; Ansorge et al., 2002; Kunde et al., 2003; Kiesel et al., 2007). Thus, these theories of subliminal processing adopt a top-down contingency (TDC) framework in which the processing of a task relevant prime stimulus evokes a specific response in an automatic manner.

In accordance with TDC accounts of subliminal processing, Vorberg and colleagues' (Vorberg et al., 2003) Accumulator Model of Priming (AMP) readily explains how a task-relevant prime can influence responses automatically. This model predicts that a prime influences responses by providing neural evidence to an "accumulator" that is tuned to a specific stimulus-response mapping. For example, if participants are required to make either a left or right response, two separate accumulators are established such that one collects neural evidence for stimuli mapped to the left response and the other collects neural evidence for stimuli mapped to the right response. If an incoming stimulus is relevant to the task (i.e. within the established stimulus-response set), it will contribute neural activity to its respective accumulator while it resides in a sensory buffer. According to Vorberg and colleagues (2003), both primes and masks are equally effective at driving the accumulators and a response is initiated as soon as the accumulated neural evidence for one response versus the other response exceeds a critical value.⁷

Taken together, TDC accounts of subliminal processing (Neumann, 1990; Kunde et al., 2003) and the AMP (Vorberg et al., 2003), suggest that if a subliminally presented stimulus is relevant to the task, it will influence responses in an automatic manner by providing neural evidence to its respective accumulator. In support of the this proposal, we have recently demonstrated that in addition to influencing response selection and initiation

⁷ Vorberg and colleagues (2003) refer to the neural evidence a stimulus provides to an accumulator as *sensory* evidence, without indicating if this activity collects in an accumulator in order to first form a perceptual representation and then activate the associated response or if the sensory evidence begins to activate a response in a more direct manner (i.e. without first forming a perceptual representation). In the original accumulator model put forth by Hanes and Schall (1996) (from which Vorberg and colleagues model the present AMP), input to an accumulator results in an increase in motor activation of the corresponding response. Specifically, according to Hanes and Schall (1996), a response is initiated once neural activity in the <u>motor area</u> of the cerebral cortex reaches a specific and constant activation threshold. Given the original accumulator model put forth by Hanes and Schall (1996) and top down contingency accounts of subliminal processing which suggest that a prime influences behaviour by activating a motor response, we discuss neural activity collecting in the accumulators as corresponding to motor activation. Thus, a response is initiated once the difference in motor activation levels between the two accumulators (representing the two response alternatives) reaches a criterion threshold.

processes within a choice reaction time task, masked primes are capable of affecting the online control of a goal-directed movement (Cressman et al., 2006). In our task, participants were given a fixed movement goal, to complete a rapid movement to a center target location. On the majority of trials a neutral prime-mask sequence was presented in the center target after movement initiation. On a small percentage of trials, the neutral prime-mask sequence was replaced with a directional arrow prime-mask sequence. The directional mask was the signal for participants to modify their pointing movement so that their movement was completed to either a left or right eccentric target location, in accordance with the direction specified by the mask arrow. Although participants remained unaware of the primes at a conscious level, kinematic analyses revealed that movement trajectories deviated in the direction of the prime (left or right) before they deviated in the direction of the visible mask.

While our results are in agreement with the principle of *conditional automaticity* as proposed within the TDC framework of subliminal processing and explained by AMP (Vorberg et al., 2003), they differed from past results typically obtained in choice reaction time tasks that emphasize response selection (Taylor and McCloskey, 1990, 1996; Klotz and Neumann, 1999; Ansorge et al., 2002, Cressman et al., 2006). Specifically, in our pointing task we observed overt responses to the prime such that pointing trajectories deviated in the direction specified by the prime, regardless of its identity or relationship to the subsequent mask. In contrast, in a choice response time task, we found that while the prime did affect response times to the mask, and hence influenced action, participants did not initiate an overt response based on the primes' identity (Cressman et al., 2006). This difference in response patterns between the two tasks suggests that task demands may change the ability of subliminal information to impact performance.

In keeping with Vorberg and colleagues' (2003) AMP of subliminal processing, we have proposed that this difference in the ability of the same subliminal stimulus to influence action may arise due to a fluctuating motor activation threshold. The level of this threshold (or Vorberg's critical value (Vorberg et al., 2003)) could be set strategically depending on the task at hand. For example, the threshold may be set at a lower level in a target-directed pointing task compared to a response time task, thus leading to overt pointing responses triggered by a prime (see Figure 1).

Our proposal suggests that the processing of subliminal stimuli differs between tasks that emphasize response selection and initiation versus on-line control and execution. In the present study, we turned our attention to the question of whether this subliminal processing can also be modulated in the pointing task. Specifically, we asked whether the processing of a prime during pointing movements would always lead to movement adjustments in the direction of the prime, or whether the prime could be processed in a more selective manner.

We examined the automaticity of prime processing in a pointing task by manipulating the probability of responding in a certain direction. The protocol was similar to our previous study (Cressman et al., 2006). Participants were given the fixed movement goal of making a rapid movement to a center target location. On the majority of trials (70%), a neutral target shape appeared within the center target and participants moved to the target shape. On the remaining 30% of trials (perturbed trials), a directional arrow prime-mask sequence was presented in the center location. The directional mask was the signal for participants to modify their pointing movement so that their finger landed in either the left or right eccentric target location, as indicated by the mask. The direction of the mask arrow was biased such that on 80% of the perturbed trials the mask arrow pointed in the same direction (either right or left). Participants were made aware of this bias and instructed that on the majority of trials in which a directional mask appeared, it would be a right (or left) arrow mask, cuing them to modify their movements and land in the right (or left) eccentric target.

Assuming that prime related activation is guided by one's intentions, as proposed by the TDC framework of subliminal processing, we predicted that manipulating the probability of a given movement would modulate the ability of a specific directional prime (i.e. prime congruent versus incongruent with the biased mask) to influence action. Specifically, we hypothesized that because the stimulus-response mapping associated with the more likely response direction would be associated with a higher baseline level of readiness (see Miller, 1988 and Gehring et al., 1992), prime pointing responses would be elicited earlier and to a greater extent in this direction, compared to the alternative, less likely response direction. Alternatively, if stimuli within the established stimulus-response set cannot be selectively processed for action, then manipulating the probability of a given movement would not modulate the degree to which the primes automatically elicit pointing responses. That is,

regardless of the identity of the prime, the prime would provide sufficient neural evidence to its putative accumulator such that the corresponding response would be initiated.

4.2 Method

4.2.1 Participants. Twelve right-handed university students (7 female, 5 male, mean age = 22.3 ± 4.8 years) with normal or corrected-to-normal visual acuity participated in this study. Participants were paid \$20 for their involvement. All participants gave informed consent, and the study was conducted in accordance with the ethical guidelines set by the University of British Columbia.

4.2.2 Apparatus. Shapes were presented in white on a black background (Viewsonic 19" monitor, 70 Hz refresh), oriented 15 degrees from the horizontal. Participants viewed the display from a distance of approximately 60 cm, with their head movements restricted by a chin-rest. The participants were positioned such that their midline was aligned with the center of the display and a home position (demarcated by a 12 mm circular marker) located centrally at the bottom of the display. In all tasks, stimuli were presented in the center of the display, located 27 cm directly above the home position. A DOS-based microcomputer was used to control stimulus presentation and data collection.

4.2.3 Stimuli. Prime shapes (4 mm x 9 mm) consisted of left-pointing and right-pointing arrows, as well as a neutral shape formed from the superimposition of the two arrows. Masks consisted of larger (23 mm x 28 mm) versions of the same shapes as the primes, with a central cutout (see Figure 1). The outer contour of the prime stimuli fit exactly within the inner contour of the central cutout of the masks. In all trials, primes were presented for 14 ms and the prime-mask stimulus-onset asynchrony (SOA) was set at 56 ms (see Figure 1). The SOA duration was selected based on pilot experiments demonstrating that it produced the strongest metacontrast masking. Masks were presented at the same central position as the primes until the pointing response was complete (approximately 400 ms).

4.2.4 Procedure. Participants completed the required tasks in two experimental sessions (Day 1 and Day 2). On the first day they performed one block of the <u>Mask Pointing</u> task. On the second day, participants completed the second half of the <u>Mask Pointing</u> task and a <u>Prime</u> <u>Identification</u> task. The <u>Mask Pointing</u> task involved making pointing movements from a home position to a center square target (4.3 cm²) 27.0 cm away. The center target was

flanked on each side by similar square targets such that the distance between the middle of the center target and the left or the right target was 7.0 cm. Participants could begin their movement to the center target anytime following the appearance of the target boxes. On 70% of the trials (direct pointing), movement of the stylus initiated the appearance of the neutral prime shape (14 ms) followed by a neutral mask shape (SOA = 56 ms) in the center target box. Participants were instructed that when this neutral mask shape appeared they were to continue pointing to the center target with a movement time goal of 300-500 ms. On the remaining 30% of trials (perturbed pointing), the prime was one of three shapes (left arrow, right arrow, neutral shape) and the mask in the center box was either a left or a right pointing arrow. Participants were instructed that the mask arrow was the signal to adjust their initial pointing movement towards the target box indicated by the mask arrow. Participants were further instructed that on the majority of perturbed trials (80%) a right (or left) arrow would appear. The direction of the higher probability mask was counterbalanced across participants such that for half the participants a right mask appeared 80% of the time and for the other half, a left mask appeared 80% of the time.

Participants began with 20 practice trials of direct pointing. They then completed 2 blocks of 250 test trials, one on each testing day, in which the 70% of direct pointing trials were randomly interspersed with the 30% of perturbed pointing trials. Movement time was measured from stylus lift-off to stylus contact with one of the target boxes. Participants were given a movement time goal of 300-500 ms and movement time feedback was provided following all direct pointing trials.

At the end of the pointing block on Day 2, participants performed a <u>Prime</u> <u>Identification</u> task. Participants were told that one of three prime shapes would be presented randomly on each trial, with equal probability, and their task was to identify them by making a 3-alternative forced choice response. They were also told that only accuracy was being measured and that response speed was no longer important. The display sequence was similar to the <u>Mask Pointing</u> task, such that on 80% of the total trials the higher probability right (or left) mask arrow was displayed. Participants viewed the prime-mask sequence with their right index finger resting below a serial response box (Psychology Software Tools, model 300). A tone sounded 400 ms following mask onset, indicating that participants could respond by pressing the left key, the center key, or the right key with their right index finger

to indicate a left pointing, neutral or right pointing prime arrow, respectively. Each participant completed 150 trials.

4.2.5 Analysis. Participants performed the pointing task with a stylus in their right hand. An infrared-emitting diode was placed at the tip of the stylus and 3D position was monitored using an OPTOTRAK (Northern Digital, Waterloo, Ontario) motion analysis system (spatial resolution 0.01 mm). The tip of the stylus was equipped with a microswitch that provided an analog signal indicating whether or not the stylus was in contact with the surface of the display. The 3D position of the stylus and the status of the microswitch were sampled at 500 Hz. Raw data from the OPTOTRAK were converted into 3D coordinates and digitally filtered using a second order dual-pass Butterworth filter with a low-pass cutoff frequency of 10 Hz. The start and end of the movement were determined by the status of the stylus.

To examine the influence of the primes on the control of pointing actions we compared pointing trajectories of the perturbed trials in which participants moved to the correct eccentric target to an average spatial trajectory computed from the direct pointing trials. The average spatial trajectory in the 2D plane was calculated for each participant from all direct pointing trials in the 2 testing blocks. The points in this trajectory were obtained by deriving the mean lateral spatial position in the x-y plane for every 2 mm of forward movement progression. If a trajectory did not have a position value at the exact spatial location required, one was obtained by linear interpolation from the closest data points. In addition, the standard deviation of the mean position in the x-direction was also calculated. The resulting mean spatial trajectory, together with its 2 standard deviation (SD) bandwidth, then became the standard against which pointing on perturbed trials were assessed (see Figure 2).

Kinematic variables (details described in Results section) were derived for perturbed trials in which participants corrected their pointing movements toward the appropriate eccentric target ($\bar{x} = 84.6\% \pm 14.7$ SD of perturbed trials). We categorized data from these perturbed trials according to the mask presented (high probability mask displayed 80% of the time vs. low probability mask displayed 20% of the time) and the prime's direction relative to the high probability mask (same as high probability mask, opposite to high probability mask, or neutral). Dependent variables were then analyzed using a 2 Group (left mask displayed on 80% of all trials, right mask displayed on 80% of all trials) x 2 Mask (high

probability mask vs. low probability mask) x 3 Prime Direction relative to the high probability mask (same, opposite, neutral) analysis of variance (ANOVA) with repeated measures on the last two factors. ANOVA did not reveal any significant effects or interactions involving the group factor for any of the variables analyzed (p > 0.05). The absence of these effects indicated that the prime-mask sequence displayed had a similar influence on performance, regardless of the direction in which the movement was biased. Thus, results will be discussed with reference to mask probability (high or low), as opposed to a specific mask direction.

For all variables examined, differences with a probability of less than .05 were considered to be significant and Tukey's Honestly Significant Difference (HSD) post-hoc tests were administered to determine the locus of the differences (alpha = .05).

4.3 Results

Mask Pointing: Subliminal primes selectively influenced the on-line control of action.

Participants completed direct pointing movements to the center target within the required movement time ($\bar{x} = 412 \text{ ms} \pm 18.1 \text{ SD}$). Figure 2 illustrates a mean spatial trajectory (open circles) computed from the direct pointing trials for 1 participant. In general, trajectories on direct pointing movements moved in a relatively straight line toward the center target. Overlaying the mean spatial trajectory in Figure 2 are individual trials in which movements were modified to the target specified by the mask (solid lines). For this participant the right mask was biased, resulting in the majority of the perturbed pointing trials being completed to the right. Although all participants were surprised to learn that mask arrows had been preceded by prime arrows upon completion of the <u>Mask Pointing</u> task, movements on perturbed trials were nevertheless influenced by the primes. In particular, the influence of a prime depended on its relationship to the biased mask.

As observed in Figure 2, only one trajectory modification away from the center target was observed on congruent trials (prime and mask pointing in the same direction) and neutral trials, regardless of the prime displayed and the direction in which the movement was completed. In contrast, on incongruent trials (prime and mask pointing in opposite directions), pointing trajectories were influenced by the prime's direction relative to the bias. Specifically, on incongruent trials in which the prime pointed in the same direction as the

high probability mask (i.e. a right prime for the participant displayed in Figure 2), participants first modified their movements in the direction of the prime before correcting their responses to the target specified by the mask. However, on incongruent trials in which a prime pointed in the opposite direction of the high probability mask (i.e. a left prime for the participant displayed in Figure 2), only one modification in trajectory was observed and that was in the direction of the visible mask.

To quantify our observation that the prime's influence on participants' pointing responses was modulated based on its relationship to the more probable mask, we measured how far away the hand was from the correct target at the time the movement was modified in its direction. Specifically, we obtained the lateral displacement from the point in time at which trajectories began to deviate toward the correct eccentric target to the termination of the movement. The trajectory adjustment point was defined as the point in time at which displacement in the lateral movement axis showed a reversal. ANOVA revealed only a marginal effect of the mask (F(1,10) = 4.991, p = 0.074), but a significant influence of the prime's direction relative to the high probability mask (F(2,20) = 21.624, p < 0.001), and an interaction between these two factors (F(2,20) = 21.613, p < 0.001). Post hoc analyses indicated a significantly larger lateral displacement for incongruent trials in which a prime pointed in the same direction as the high probability mask compared to any other prime-mask combination (Figure 3). None of the other prime-mask combinations, including incongruent trials in which a prime pointed in the opposite direction to the high probability mask, differed from each other. Thus, trajectory deviations away from the correct target were only observed on incongruent trials in which the prime pointed in the same direction as the high probability mask.

It is evident from these findings that participants did not respond to the primes in an automatic or stereotypic manner. The influence of the prime on pointing responses differed depending on whether or not it pointed in the same direction as the high probability mask. In attempt to explain how the directional primes selectively influenced visuomotor processing, we examined the timing of trajectory modifications on all perturbed trials. An estimate of the time at which perturbed pointing movements were first modified from the center target was obtained by contrasting individual perturbed trajectories with their corresponding mean direct pointing spatial trajectories. If a perturbed path crossed the 2 SD bandwidth of the mean

spatial trajectory it was considered to have been modified. The time of the first trajectory modification was then established by determining the time corresponding to the point at which displacement in the lateral movement axis first reached a reversal point in the trajectory. ANOVA revealed significant main effects (mask: F(1,10) = 0.022, p = 0.005 and prime direction: F(2,20) = 69.53, p < 0.001). The interaction was not significant (F < 1) (Figure 4). Trajectories were modified earlier in the direction of the higher probability mask ($\bar{x} = 321 \text{ ms} \pm 16 \text{ SD}$) compared to the low probability mask ($\bar{x} = 335 \text{ ms} \pm 21 \text{ SD}$). Furthermore, Tukey's HSD analyses revealed that modifications occurred at a significantly shorter latency on trials in which the prime pointed in the same direction as the high probability mask ($\bar{x} = 306 \text{ ms} \pm 22 \text{ SD}$), compared to when the prime pointed in the opposite direction to the high probability mask ($\bar{x} = 326 \text{ ms} \pm 21 \text{ SD}$) or was neutral ($\bar{x} = 352 \text{ ms} \pm 16 \text{ SD}$). Trials in which the prime pointed in the opposite direction to the high probability mask ($\bar{x} = 326 \text{ ms} \pm 21 \text{ SD}$) or was neutral ($\bar{x} = 352 \text{ ms} \pm 16 \text{ SD}$). Trials in which the prime pointed in the opposite direction to the high probability mask ($\bar{x} = 326 \text{ ms} \pm 21 \text{ SD}$) or was neutral ($\bar{x} = 352 \text{ ms} \pm 16 \text{ SD}$). Trials in which the prime pointed in the opposite direction to the high probability mask also differed significantly from trials with a neutral prime.

Prime Identification: Primes were invisible to participants.

Participants' subjective reports indicated they were unaware of the presence of the primes while completing the <u>Mask Pointing</u> task. To determine their ability to consciously discriminate between the primes we had participants perform a <u>Prime Identification</u> task. It should be noted, however, that the <u>Prime Identification</u> task differed from the <u>Mask Pointing</u> task both in terms of prime awareness and task goal. In the <u>Mask Pointing</u> task, participants were not explicitly aware of the presence of the primes and their primary goal was to make a movement in accordance with the identity of the mask. In contrast, in the <u>Prime Identification</u> task, participants' sole responsibility was to identify which prime had been presented.

Mean accuracy collapsed across all prime-mask sequence combinations was $44.8\% \pm 10.7$ (SD). A chi-square goodness-of-fit test revealed that this proportion of correct responses did not differ from chance at the p = 0.05 level ($\chi^2 = 0.713$). Thus, even when participants were explicitly aware of the presence of the primes and could focus all of their attention on attempting to identify which prime had been displayed, they incorrectly reported the prime's identity on the majority of trials. Combining these results with participants'

subjective reports, we are confident that the primes were "invisible" to participants during the <u>Mask Pointing</u> task.

4.4 Discussion

In the current study we investigated the automaticity of subliminal visuomotor processing in a goal-directed pointing task by manipulating the baseline probability that a given directional mask would appear in a prime-mask sequence. Previous studies examining the influence of probability manipulations on responses completed to visible stimuli have demonstrated that higher probability events lead to faster responses (see LaBerge et al., 1969; Blackman, 1972; Hawkins et al., 1973; Heuer, 1982). Thus, we expected earlier deviations in the direction corresponding to the higher probability mask. However, it was unclear how this intentional response bias would influence the processing of subliminal information.

To determine the influence of subliminal stimuli on action we examined pointing trajectories for modifications in response to the prime. Of particular interest were the incongruent prime-mask trials, as it was only in these trials that we could be assured that we were looking at direct evidence of priming while pointing actions were ongoing. The neutral and congruent prime-mask trials did not afford this opportunity since the prime-mask sequence was expected to give rise to only one change in trajectory from the center target. Therefore, based on the trajectory profiles of these trials, we could not conclude if a modification from the center target resulted from processing of the prime or the visible mask that followed later in time. However, by examining the pointing trajectories in the incongruent trials and comparing the timing of trajectory modifications across all perturbed trials, we could infer if primes were processed for the control of action.

We have shown previously that when reaching trajectories are to be modified equally often to the left and to the right, directional primes have a similar influence on movement. In particular, participants modify their movements on-line in response to a directional prime (see Cressman et al., 2006). We explained our previous results by amending the top-down contingency (TDC) framework of subliminal processing and put forth that task constraints may modulate the impact of subliminal stimuli on action. Specifically, in keeping with Vorberg and colleagues' accumulator model (Vorberg et al., 2003), we assumed that a prime automatically provides neural evidence to an "accumulator" tuned to a specific stimulus-

response mapping, regardless of task requirements. However, we suggested that the level of neural activity required to initiate a response could be selectively set based on task demands. In the case of our pointing task, it could be set at a level that allowed a response to be initiated according to a prime's identity. Thus, our model of priming assumed that after the level of neural activity was established based on the task at hand (e.g. pointing movement versus a choice response time task), a prime would contribute to an accumulator, and hence to a response, in an automatic manner. From the current investigation, it is apparent that the processing of the prime for action can be modulated, even within a task.

We observed different responses on trials in which the prime pointed in the same direction as the high probability mask (and thus the direction in which participants were more likely to adjust), compared to when the prime pointed in the opposite direction. Specifically, we found that movement trajectories were adjusted in response to the prime when it pointed in the high probability direction, but not when it pointed in the opposite direction. These results demonstrate that during the pointing task, the visuomotor processing of the prime was dependent on its relation to task-relevant expectations (i.e., whether the prime's identity was consistent with the participant's intentional bias). This indicates that the processing of subliminal information for action is subject to modulation by intention.

In order to account for how this change in subliminal processing may have arisen, we also examined the timing of trajectory modifications to determine the time-course of the processing of the masked primes. Although initial modifications in trajectories were influenced by both the mask and the prime's relation to the high probability mask, there was no interaction between these factors (see Figure 4). The earliest movement modifications occurred when the prime pointed in the same direction as the high probability mask. The latest modifications occurred when the prime was neutral relative to the bias. Furthermore, intentional modifications occurred earlier in response to a high probability mask compared to a low probability mask, independent of the preceding prime. For example, even on trials in which a neutral prime was displayed, this influence of the participants' intentional bias was evident. The timing difference between neutral prime trials could not have arisen due to changes in prime processing, as there was only one neutral prime. Rather, the difference in results between the neutral trials must reflect differences in visuomotor processing of the visible masks as a consequence of the instructions provided.

Taken together, it is evident from the present results that task instructions (i.e. intention) must be taken into account in an explanation of how primes can be selectively processed for action. Previous research demonstrating that a higher probability event is responded to more quickly than an alternative, less likely response has suggested that differences between the two responses arise due to advanced preparation of the more probable response prior to stimulus onset (Bertelson and Barzeele, 1965; Laming, 1969). In accordance with this proposal, Miller (1988) demonstrated that in a two-choice reaction time task (75% left vs. 25% right responses), the time-course and direction of the lateralized readiness potential (an index of selective motor activation) was indicative of participants preparing the response associated with the high-probability event prior to the onset of the imperative stimulus. Furthermore, Miller (1988) also found that when stimulus onset, even on trials in which the low probability stimulus was displayed (see also Gehring et al., 1992).

In attempt to explain the influence of subliminal stimuli on performance in the present experiment within an accumulator-based model, while taking into account previous research examining probability manipulations on responses to visible stimuli, we propose that participants selectively adjust the activation level associated with a particular response based on the instructions provided (see Figure 1b). For example, if a participant is instructed that on the majority of trials a right response will be required, the neural activity associated with the right accumulator is increased before the trial has even begun. This predisposition for the right response, pre-sets the system to favour the high probability response at the time of prime presentation (i.e. the difference in response activation between the accumulators is weighted to favour the more likely response). Because of this initial activation, our model predicts that movements will be initiated earlier to the right than the left when the masks are preceded by a neutral prime (or even when presented alone). Furthermore, this threshold difference between the two accumulators at the time of stimulus onset will also impact the influence of left and right primes on responses. The neural activity associated with a right prime could cause the difference in accumulators to surpass the required threshold, leading to overt responses associated with the right prime. In contrast, because participants' advanced preparation of the right response must be counteracted in order for a left response to be

initiated, a greater amount of activity must be accumulated. Thus, neural activity associated with the left prime would not achieve this threshold level before input from the mask began to activate its associated response, and hence, left prime responses would not be initiated.

The predictions of our proposed version of the accumulator model are consistent with both the spatial and temporal characteristics of the pointing trajectory modifications observed in the present experiment. Specifically, trajectories were only modified in the direction of the prime when it pointed in the same direction as the high probability mask and these modifications occurred at a similar latency, regardless of the mask direction. We assume that subliminal information about a prime was processed along the visual-motor system and the resulting prime-related neural activity began to activate its associated response (i.e. fill the associated accumulator). However, the impact of a particular subliminal stimulus on action was also dependent on differences in the neural evidence necessary to initiate a response. Since participants were made aware of the fact that the majority of their perturbed movements were more probable in a certain direction, it seems reasonable to assume that participants used this information to guide their responses and adjust the neural evidence necessary to commit to a response accordingly.

Thus, in our pointing task we assume that the shift in the influence of the primes on action was driven by one's awareness of the task constraints. A question that arises from this proposal is whether or not the activation level of a specific response (or even responses in general), and hence the impact of subliminal stimuli on action, can be altered even when one is not explicitly aware of task constraints. Recent work by Jaskowski and colleagues (2003) suggests that the impact of subliminal information on action can change even in situations in which participants are unaware of a given prime-mask manipulation. In their study a series of subliminal primes were presented and participants were required to make a left or right key-press response based on the location of the main mask stimulus. In addition to finding that the prime series had additive priming effects, Jaskowski and colleagues (2003) demonstrated that performance changed with the proportion of congruent and incongruent trials displayed (i.e. 80% congruent trials versus 20% congruent trials). Participants were faster to respond when the primes accurately predicted which response was required 80% of the time versus 20%. According to Jaskowki et al., participants strategically adapted their response criterion so that they would not commit too many errors. It remains to be seen if

similar findings can be observed in a priming task in which a single prime is presented and participants are to respond according to the identity of a stimulus.

4.5 Conclusion

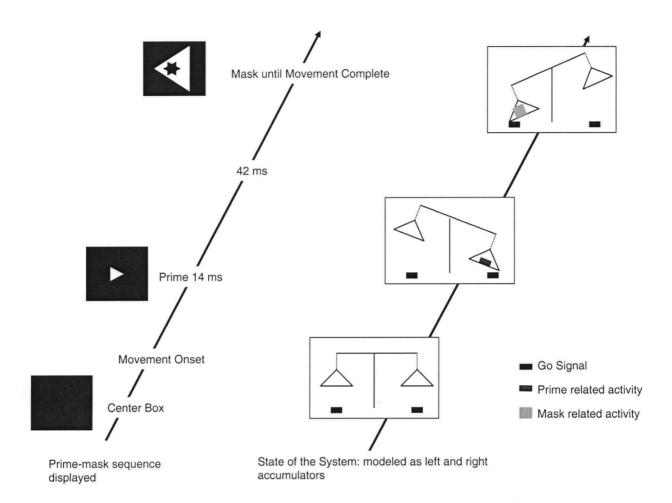
When participants are asked to adopt an intentional bias in the on-line control of their goal-directed movements, only masked primes that are consistent with the bias lead to unconscious modifications of action. Thus it appears that the processing of subliminal information for action can be modulated, such that it is sensitive to the conscious expectations of the participant. We propose that this adaptation arises due to modifications in the level of neural evidence required for a particular response to be initiated as a result of participants selectively preparing the more likely response in advance of stimulus onset.

4.6 Bridging Summary

The difference in response patterns arising in (1) Study 1 between the reaction time and pointing task and (2) Study 3 between the different directional primes indicates that subliminal visuomotor processing is dependent on task constraints. For example in the reaction time task of Study 1, prime-related activity influenced responses to the visible mask stimulus presented later in time, without taking over control of the movement. In contrast, in the pointing task, subliminal events took over the control of the goal-directed movement such that responses were initiated in the direction cued by the prime. Furthermore, in Study 3, the influence of a particular directional prime on action was dependent on its ability to correctly predict the upcoming response. Taken together, these results suggest that subliminal visuomotor processing can be modulated (i.e. a prime does not influence performance in a set, automatic manner).

In the fourth study we questioned if modifications in subliminal processing would arise when task constraints were manipulated at an unconscious level. Specifically we investigated the *automaticity* of unconscious processing within a reaction time task in which the prime-mask sequence was manipulated at a conscious and unconscious level. Four separate metacontrast masking reaction time experiments were conducted. In each experiment participants were required to press left and right keys in response to left and right

arrows respectively. In contrast to previous metacontrast masking reaction time experiments, the relationship between the prime and mask was systematically varied between the four experiments. The first experiment was a replication of a "typical" metacontrast masking reaction time task, in which all stimuli were displayed with equal probability. Results from this experiment were regarded as a baseline measure of participants' performance. In the second experiment we biased the mask displayed and instructed participants that a particular response would be required on the majority of trials (e.g. left mask biased = left response required). In the third experiment, left and right responses were required equally often, but, on the majority of trials a specific directional prime was displayed. Finally, in the fourth experiment we varied the proportion of congruent prime-mask trials displayed. Because the stimulus events were manipulated at an unconscious level in Experiments 3 and 4, we predicted, in accordance with top-down contingency accounts of unconscious processing, that prime-related activity would have a similar influence on performance as in Experiment 1.



<u>Figure 4.1</u>. (A) Overview of the proposed Accumulator Model of Priming. If an incoming stimulus is in the established stimulus-response set, it will contribute neural evidence to its respective accumulator while residing in a buffer (e.g. a right arrow will contribute neural evidence to a right accumulator). Both primes and masks are equally effective at driving the accumulators. We have proposed that in a pointing task, primes contribute sufficient neural activity such that a motor activation threshold (computed as the difference in the activation levels between the two response alternatives) is achieved and a response is initiated in response to the prime. Note: the timing between the prime-mask sequence displayed on the left and the state of the system modeled as accumulators on the right does not correspond directly. Changes in the level of activation of the accumulators would be delayed with respect to stimulus onset.

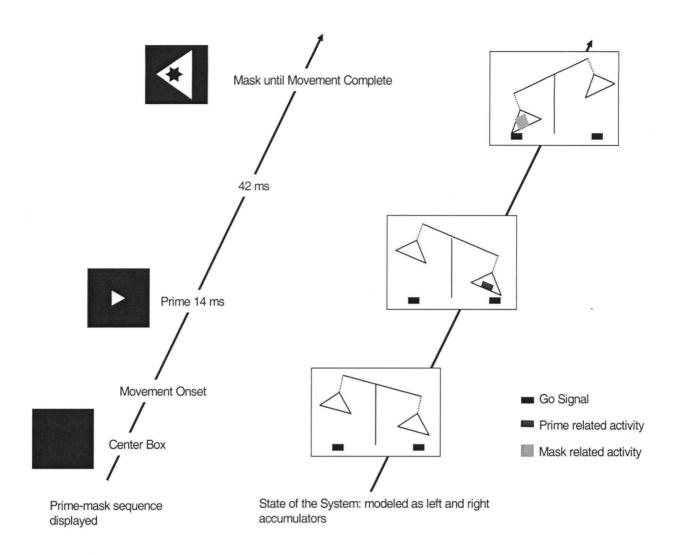
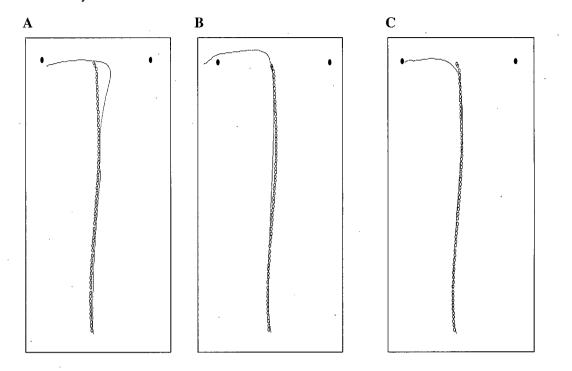
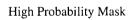


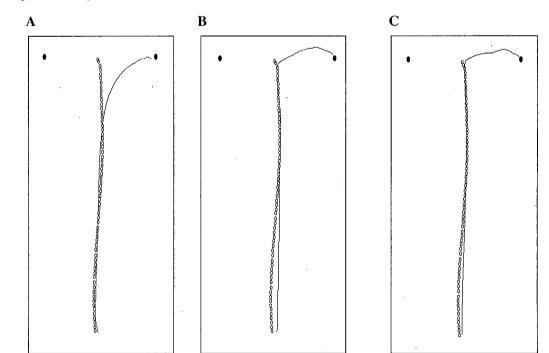
Figure 4.1. (**B**) To account for our current findings we propose that participants selectively activate the response in the direction of the biased mask, such that at the time of stimulus onset the difference in activation levels between the two response alternatives favours the more probable response. Both primes and masks are still equally effective at driving the accumulators; however, modifications in the direction of the prime are only observed on trials in which the prime is pointing in the same direction as the biased mask. On these trials activity from this prime adds to the initial activation and achieves the required threshold value. In contrast, on trials in which the prime points in the opposite direction as the biased mask, prime related activity is not capable of achieving the required threshold value before input from the mask begins to activate its associated response, as additional neural activity is required to counteract the initial activation of the more probable response.

<u>Figure 4.2.</u> Examples of a mean direct spatial trajectory (open circles) and individual perturbed spatial trajectories (solid line) under each of the prime-mask conditions in which a low probability mask was displayed (top row) or a high probability mask was displayed (bottom row) ((A) prime pointing in the same direction as the high probability mask, (B) neutral prime or (C) prime pointing in the opposite direction to the high probability mask). The center of the eccentric target boxes are indicated by annuli (the center target box is not visible). For this participant the right mask was displayed on the majority of trials (80%). Note that an initial incorrect trajectory modification was only observed on the incongruent trial in which a prime pointing in the same direction as the high probability mask (i.e. a right prime) was displayed.

Low Probability Mask







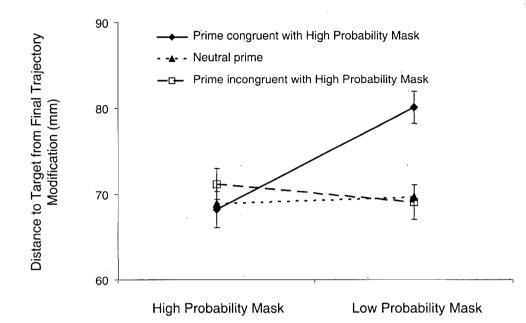


Figure 4.3. Effect of the prime-mask sequence on lateral displacement from the point in time at which trajectories began to deviate toward the correct eccentric target to the end of the movement. Error bars denote standard errors.

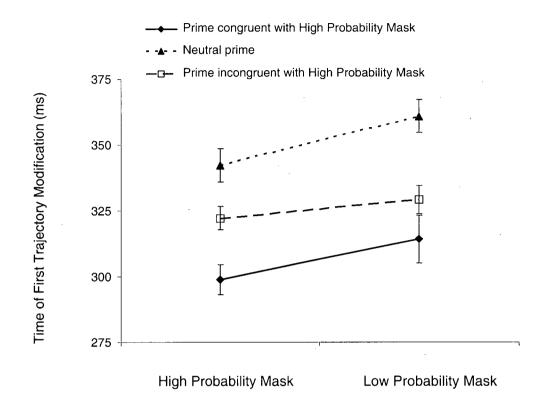


Figure 4.4. Effect of the prime-mask sequence on the time of the first trajectory modification from the center target. Error bars denote standard errors.

4.8 References

Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-545.

- Bertelson, P., & Barzeele, J. (1965). Interaction of time uncertainty and relative signal frequency in determining choice reaction time. *Journal of Experimental Psychology*, 70, 448-451.
- Blackman, A.R. (1972). Influence of stimulus and response probability on decision and movement latency in a discrete choice reaction task. *Journal of Experimental Psychology*, 92, 128-134.
- Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.
- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1595.
- Cheesman, J. & Merikle, P.M. (1986). Distinguishing conscious from unconscious perceptual processes. *Canadian Journal of Psychology*, 40, 343-367.
- Cressman, E.K., Franks, I.M., Enns, J.T., & Chua, R. (2006). On-Line Control of Pointing is Modified by Unseen Visual Shapes. *Consciousness and Cognition*, in press.

Damion, M.F. (2001). Congruity effects evoked by subliminally presented primes:

Automaticity rather than semantic priming. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 154-165.

- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P.-F., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597-600.
- Enns, J.T., & DiLollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Gehring, W.J., Gratton, G., Coles, M.G.H., & Donchin, E. (1992). Probability effects on stimulus evaluation and response processes. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 198-216.

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

- Hawkins, H.L., MacKay, S., Holley, S., Friedin, B., & Cohen, S. (1973). Locus of the relative frequency effect in choice reaction time. *Journal of Experimental Psychology*, 101, 90-99.
- Heuer, R.H. (1982). Choice between finger movements of different and identical form: The effect of relative signal frequency. *Psychological Research*, 44, 323-342.
- Jaskowski, P., Skalska, B., Verleger, R. (2003). How the self controls its "automatic pilot" when processing subliminal information. *Journal of Cognitive Neuroscience*, 15, 911-920.
- Kahneman, D. (1968). Methods, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70, 404-425.
- Kiesel, A., Kunde, W., & Hoffmann, J. (in press). Mechanisms of subliminal response priming. *Advances in Cognitive Psychology*.
- Kunde, W., Kiesel., A., & Hoffmann, J. (2003) Conscious control over the content of unconscious cognition. *Cognition*, 10, 198-205.
- LaBerge, K., Legrand, R., & Hobbie, R.K. (1969). Functional identification of perceptual and response biases in choice reaction time. *Journal of Experimental Psychology*, 79, 295-299.
- Laming, D.R.J. (1969). Subjective probability in choice-reaction time experiments. *Journal* of Mathematical Psychology, 6, 81-120.
- Miller, J. (1998). Effects of stimulus-response probability on choice reaction time: Evidence from the lateralized readiness potential. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1521-1534.
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-215.
- Neumann, O., & Klotz, w. (1994). Motor responses to nonreportable, masked stimuli:
 Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Schmidt, T. (2000). Visual perception without awareness: Priming responses by color. In T. Metzinger (Ed.), Neural correlates of consciousness (pp. 157-170). Cambridge, MA: MIT Press.

- Schmidt, T. (2002). The finger in flight: Real-time motor control by visually masked color stimuli. *Psychological Science*, 13, 112-118.
- Taylor, J.L., & McCloskey, D.I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology*, 63, 439-445.
- Taylor, J.L., & McCloskey, D.I. (1996). Selection of motor responses on the basis of unperceived stimuli. *Experimental Brain Research*, 110, 62-66.
- Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. Proceedings of the National Academy of Sciences of the United States of America, 100, 6275-6280.

CHAPTER 5

STUDY 4: Pushing the limits of unconscious processing: Evidence for an adaptive visuomotor system⁸

5.1 Introduction

Visual stimuli presented below the threshold of conscious awareness can influence motor behaviour. This phenomenon is readily demonstrated in reaction time (RT) tasks in which a visual stimulus is masked from awareness by a subsequent target stimulus. For example, in a recent study by Vorberg and colleagues (2003), participants were instructed to respond as quickly as possible to the visual presentation of a large arrow-shaped stimulus. Specifically, participants responded with a left or right key press corresponding to the left or right direction of the arrow. On each trial, the large arrow (*the mask*) was preceded by a briefly displayed smaller arrow (*the prime*) that pointed in the same (congruent) or opposite (incongruent) direction. Although the prime was made unavailable to the conscious system by metacontrast masking (for reviews of metacontrast masking see Kahneman, 1968; Breitmeyer, 1984; Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000), participants responded more quickly to the mask stimulus on congruent trials in comparison to incongruent trials (a finding dubbed the "metacontrast dissociation").

Reaction time (RT) paradigms giving rise to the metacontrast dissociation provide the opportunity to explore the extent to which unconscious information processing can contribute to action. According to current theories (e.g. the theory of Direct Parameter Specification (DPS): Neumann, 1990; Neumann & Klotz, 1994; the Action Trigger Hypothesis: Kunde et al., 2003; Kiesel et al., 2007), a stimulus presented below the threshold of conscious awareness will influence performance automatically, if it is relevant to the task (e.g. an arrow in the study by Vorberg et al. (2003) described above). Thus, these theories adopt a top-down contingency (TDC) framework, and place restrictions on the ability of unconscious events to influence performance. For example, according to current TDC accounts, the processing of a task relevant prime results in the immediate activation of the associated response and hence, will influence behaviour in a "conditionally automatic" manner. The automaticity of the prime-related response is further dictated by the assumption that the prime is not available to the information processing system as a whole but rather processes

⁸ A version of this chapter will be submitted for publication.

associated with the prime are restricted to comparing the incoming stimulus with stimulusresponse alternatives and activating a corresponding response when appropriate (Neumann, 1990; Ansorge et al., 2002, Kunde et al., 2003; Kiesel et al., 2007).

In support of the *conditional* influence of subliminal information on action proposed by TDC accounts, Ansorge and colleagues (2002) have demonstrated that a spatial prime stimulus does not influence performance when participants are required to make a response based on a specific feature of the mask stimulus (e.g. indicate if the mask consists of vertical or horizontal lines) which is not present in the prime (see also Enns and Oriet, 2007). Furthermore, Kunde et al. (2003) have illustrated that priming effects can extend to situations in which multiple stimuli are mapped to a particular response, provided that the subliminal information is within the established, and expected, stimulus-response mapping (see also Ansorge, 2004; Ansorge and Neumann, 2005). In the task employed by Kunde and colleagues (2003), participants were instructed to press a left or right key in response to a number less than or greater than 5, respectively. Although the only numbers used as target masks were 1, 4, 6 and 9, Kunde and colleagues (2003) observed priming effects for all prime stimuli (numbers 1 through 9, excluding 5). Thus, even the numbers 2, 3, 7 and 8 which had been mapped to a particular response but were never responded to (or available) at a conscious level, influenced action (see also Naccache and Dehaene, 2001). Moreover, the priming effect was abolished when the notation between the primes and masks varied and the primes were presented in an unexpected notation (e.g. primes were presented in number words, and participants were to respond to target masks displayed in Arabic notation).

From the studies discussed above, it is evident that the influence of a subliminal stimulus on action is dependent on its relationship to the target mask stimulus, and hence participants' intentions. In particular, a prime will influence behaviour, only if it is within an established stimulus-response mapping. According to TDC accounts, this mapping is established based on a pre-emptive, consciously mediated control mechanism, which links a particular stimulus (or stimuli) with a given response as a consequence of instructions provided. However, while it is evident that the influence of a prime is contingent on one's intentions, previous research does not dictate that this influence need (or should) be regarded as automatic (i.e. that the prime impacts performance in a set manner if it is within an established stimulus-response mapping). In fact, recent work by Jaskowski and colleagues

(Jaskowski et al., 2003; Wolbers et al., 2006), suggests that the influence of subliminal stimuli on action may be modulated depending on the ability of a task relevant prime to correctly predict the upcoming response (see also Bodner and Masson, 2001, 2003). Furthermore, in a task by Bodner and Dypvik (2005) in which participants were to categorize target numbers as odd or even, results demonstrated that a subliminal prime had a greater influence on performance when it was identical to the mask stimulus (e.g. prime-mask sequence =1-1) compared to when it merely indicated that the same response was required (e.g. prime-mask sequence = 1-3). Thus, perhaps current TDC accounts of subliminal processing place too great of restrictions on processes associated with subliminal information (i.e. unconscious events associated with the prime may not be limited to the automatic activation of a corresponding response).

5.1.1 Overview of Experiments

The goal of the present research was to investigate the intention-dependent automaticity of the unconscious system as outlined by TDC-based accounts of subliminal processing. Central features of theories that posit a TDC framework include the roles played by conscious intention, unconscious stimulus processing, and more importantly, the potential interaction between the two. Thus, in the present work, we were particularly interested in subliminal response priming under conditions in which conscious events and subliminal events were varied independently. Closely integrated with these experimental manipulations was an examination of the impact of changes in the pattern of prime-mask congruency.

In the first experiment, we began with a typical metacontrast masking protocol in which primes and masks were displayed with equal probability. The goal of this experiment was to replicate the "metacontrast dissociation" and obtain important baseline RT effects for subliminally presented stimuli using our protocol. In the second experiment we made participants aware of a large bias in the probability distribution of the target stimuli in order to determine whether one's expectations regarding the upcoming response would mediate the impact of masked primes on action. According to TDC accounts, subliminal information influences responses automatically if it is relevant to the task at hand. In this task, while all information was relevant to the task, the degree of relevance varied between stimuli. Thus, we were interested in determining whether intention-dependent subliminal priming was

sensitive to response biases. In other words, would an observer's intentional predisposition towards a favoured motor response influence the impact of subliminally presented primes?

In the next experiment (Experiment 3), we examined whether intention-dependent subliminal priming was sensitive to changes in stimulus events that occurred outside of conscious awareness. In order to examine modifications in responses to subliminal events, we investigated if manipulations in the frequency of occurrence of an unconscious event (i.e. the prime displayed) could lead to changes in priming effects. In the final experiment (Experiment 4) we examined the impact of intention-dependent subliminal priming on action when the relationship between conscious and unconscious events was manipulated. Specifically, we manipulated the proportion of trials in which the prime and mask were congruent. In both Experiment 3 and 4, conscious events were similar to Experiment 1 (i.e. left and right targets were presented on an equal number of trials). Thus, the manipulations of the prime-mask sequence displayed occurred outside of participants' awareness. According to TDC accounts, results of Experiments 3 and 4 should be similar to Experiment 1. Specifically, the same overall congruency effect should be observed and primes were expected to have a similar impact on performance, as the processing of subliminal information is constrained by its relationship with established stimulus-response mappings.

5.2 **Experiment 1: Baseline performance**

The goal of the first experiment was to establish the impact of subliminal primes on responses to mask stimuli when the prime-mask sequence was displayed in a typical prime-mask RT task.

5.2.1 Methods

5.2.1.1 Participants. Eleven right-handed university students (7 female, 4 male, mean age = 21.9 ± 2.2 years) participated in this study. All participants had normal or corrected-to-normal visual acuity and were reimbursed for their involvement (\$20). Participants provided informed consent and the studies was conducted in accordance with the ethical guidelines set

by the University of British Columbia. Data from one participant were excluded for failure to follow task instructions.

5.2.1.2 Stimuli. Prime shapes (4 mm x 9 mm) consisted of a left-pointing and right-pointing arrow, as well as a neutral shape formed from the superimposition of the two arrows. Masks consisted of larger (23 mm x 28 mm) versions of the same shapes as the primes, with a central cutout (see Figure 1). The outer contour of the prime stimuli fit exactly within the inner contour of the central cutout of the masks. In all trials, primes were presented for 14 ms and the prime-mask stimulus-onset asynchrony (SOA) was set at 56 ms. The SOA duration was selected based on pilot experiments demonstrating that it produced the strongest metacontrast masking. Masks were presented at the same central position as the primes until a response was complete (approximately 400 ms).

5.2.1.3 Apparatus. Shapes were presented in white on a black background (Viewsonic 19" monitor, 70 Hz refresh), oriented 15 degrees from the horizontal. Participants viewed the display from a distance of approximately 60 cm, with their head movements restricted by a chin-rest. The participants were positioned such that their midline was aligned with the center of the display and a serial response box (Psychology Software Tools, Model 300) located at the bottom of the display. In all tasks, stimuli were presented in the center of the display, located 27.0 cm directly above the center of the response box. A DOS-based microcomputer was used to control stimulus presentation and data collection.

5.2.1.4 Procedure. Participants performed two tasks in one experimental session. The first task was a <u>Mask Reaction Time</u> task. Participants rested their left and right index fingers on the left key and right key of the response box, respectively. Participants were instructed to direct their attention to a fixation point at the center of the display monitor (500-1000 ms) and respond as quickly and as accurately as possible to the direction of the mask arrow (left or right) with the corresponding key press. Mask arrows were preceded by a left pointing, right pointing, or neutral prime arrow (14 ms). Prime-mask SOA was 56 ms.

To obtain an index of the impact of our prime stimuli on performance, neutral, left and right primes preceded left and right masks with equal probability. Left and right masks were also presented on an equal number of trials. On 50% of the trials in which a directional prime was displayed, the prime was followed by a congruent mask. Participants completed one block of 120 trials. Table 1 provides a summary of the prime-mask combinations displayed in each experiment and the number of trials completed per condition.

After completing the <u>Mask Reaction Time</u> task, participants performed a <u>Prime</u> <u>Identification</u> task. In this task, participants were made aware that a left, right or neutral prime shape would be presented randomly on each trial, with equal probability, and their task was to identify them. Participants were also told that only accuracy was being measured and response speed was no longer important. Similar to the <u>Mask Reaction Time</u> task, the prime was displayed for 14 ms and the prime-mask SOA was 56 ms. Participants viewed the prime-mask sequence with their right index finger resting below the serial response box. A tone sounded 400 ms following mask onset, indicating that participants could respond by pressing the left key, the center key, or the right key with their right index finger to indicate a left pointing, neutral or right pointing prime arrow, respectively.

5.2.1.5 Data Analysis. The variables of interest were reaction time (RT) and percentage of errors completed. Trials in which participants pressed the incorrect key in the <u>Mask Reaction Time</u> task were treated as errors and excluded from RT analyses. In addition, for each participant a range in response times was established and trials in which RT fell outside the corresponding range were excluded from all analyses (< 2.0% of all trials). The range in a participant's response times was determined by first calculating a mean RT for each prime-mask combination displayed and corresponding standard deviation. A participant's response time and subtracting 3 times the participant's mean standard deviation (calculated by averaging the standard deviations obtained in each prime-mask combination) to the prime-mask combination with the greatest and smallest mean RT, respectively. In order to analyze the percentage of errors completed for each prime-mask combination, the data were first normalized using an arcsine-root transformation.

For all variables examined, analysis of variance results are reported with Greenhouse-Geisser-corrected p values. Differences with a probability of less than .05 were considered to be significant and Tukey's Honestly Significant Difference (HSD) post-hoc tests were administered to determine the locus of the differences (alpha = .05). The p values of nonsignificant results are presented only when the corresponding F value exceeds 1.

5.2.2 Results

Mask Reaction Time Task. Figure 2a displays mean correct reaction times (RT) for both left and right responses as a function of the prime's relation to the mask (congruent, incongruent or neutral). As shown in Figure 2a, RT to the mask was greatly influenced by prime congruency. Furthermore, the impact of prime congruency appeared to be of a similar magnitude, regardless of whether participants were responding to the left or right mask. Consistent with these observations, a 2 mask (left, right) by 3 prime congruency (congruent, incongruent, neutral) repeated measures analysis of variance (ANOVA) revealed a significant main effect for prime congruency, F(2,18) = 155.611, p < .001, that was independent of the mask displayed (Mask: F(1,9) < 1; Mask by Prime Congruency: F(2,18) < 11). Post-hoc mean comparisons revealed that RT was faster when masks were preceded by congruent primes compared to incongruent or neutral primes. Furthermore, mean RT was slower on incongruent trials than neutral trials. In order to determine the impact of the primes on performance, we collapsed RT across left and right responses and calculated the congruency effect as the difference in mean RT on congruent trials compared to incongruent trials. Based on this congruency score, the magnitude of the primes' impact on performance was approximately 56 ms.

In addition to RT, we examined participants' performance accuracy. Overall, participants were very accurate in the <u>Mask Reaction Time</u> task (> 96% correct overall). Errors on the remaining trials were not equally distributed across all types of trials (the mean percentage of errors for each prime-mask combination are provided in Table 2). ANOVA revealed a significant main effect for prime congruency (F(2,18) = 16.794, *p* < 0.001), that was independent of the mask displayed (Mask: F(1,9) < 1, Mask x Prime Congruency: F(2,18) < 1). Post-hoc analyses indicated that participants committed a significantly greater number of errors on trials in which the prime and mask were incongruent compared to any other prime-mask combination.

<u>Prime Identification Task</u>. Chance performance in this task was 33% (given the three equally likely alternatives). Mean accuracy collapsed across all prime-mask sequence combinations was $39.7\% \pm 7.3$ (SD). A chi-square goodness-of-fit test revealed that this proportion of correct responses did not differ from chance at the p = 0.05 level ($\chi^2 = 0.181$).

5.2.3 Discussion

In Experiment 1, we replicated the metacontrast dissociation. We found that even though participants were unaware of the primes, responses to the mask were influenced by information contained in the prime. This influence was independent of the mask displayed and hence the required response. Specifically, we found a reaction time benefit for congruent primes and a reaction time cost for incongruent primes. The overall impact of the primes on performance, as reflected by the mean congruency score, was approximately 56 ms, a magnitude equivalent to the prime-mask onset asynchrony. Finally, participants made the most errors on trials in which the prime and mask were incongruent.

The results from Experiment 1 fit within a TDC framework of subliminal processing, as responses to the mask were influenced by its relationship to a preceding subliminal prime. In accordance with TDC accounts (i.e., the DPS and Action Trigger hypotheses), we propose that participants prepared to initiate left and right motor responses to left and right (mask) arrows, respectively. If a directional (prime) arrow was displayed, it began to activate its corresponding response, regardless of participants' conscious awareness. However, prime-related motor activity did not appear to achieve a required threshold (e.g., Vorberg et al., 2003), necessary to initiate an overt response, but rather biased responses to the mask. Thus, on congruent trials prime-related processing resulted in faster RTs, as prime processing activated the correct response, while on incongruent trials, RT was slower because prime processing led to the initial activation of the incorrect response.

5.3 Experiment 2: The influence of an intentional bias on subliminal processing

In Experiment 2 we questioned if manipulating participants' expectations regarding the upcoming response (i.e. intentions) would influence the impact of subliminal processing on performance. Similar to Experiment 1, directional and neutral primes were displayed with equal probability and participants were instructed that they were to press a left or right key in response to the direction of an arrow mask. However, in contrast to Experiment 1, participants were told that one of the directional mask arrows would be displayed, and the corresponding response required, on the majority of trials (80%). For example, participants were instructed that on 80% of the trials a left mask arrow would appear and a left key press would be required.

Previous investigations examining the influence of probability manipulations on responses to visible stimuli have shown that higher probability events lead to faster responses (see LaBerge et al., 1969; Blackman, 1972; Hawkins et al., 1973; Heurer, 1982). In order to explain these findings, researchers have suggested that a higher-probability response is prepared prior to stimulus onset (Bertelson and Barzeele, 1965; Laming, 1969). In support of this proposal, Miller (1988) derived the lateralized readiness potential (LRP: an index of selective motor activation) during the foreperiod of a two-choice reaction time task in which left and right responses were completed with unequal probability (e.g. 75% left responses vs. 25%). Miller found that the LRP waveforms were indicative of participants preparing the response associated with the high-probability stimulus prior to the onset of the imperative stimulus. Furthermore, Miller (1988) also found that when stimulus onset, even on trials in which the low probability stimulus was displayed (see also Gehring et al., 1992).

Consistent with previous work demonstrating that higher probability events lead to faster responses, we hypothesized that RT to the more probable biased mask (i.e. the mask displayed on 80% of trials) would be faster than responses initiated to the less probable mask (i.e. the mask displayed on 20% of trials). However, it was unclear how the conscious manipulation of response tendency would influence the impact of subliminal information on action. According to TDC accounts, unconscious information is contingent on participants' intentions. Thus, if participants were more inclined to initiate a particular response, we expected that the influence of a prime on performance may vary depending on its relationship to the biased mask. For example, primes pointing in the same direction as the higher probability mask were expected to have a greater influence on action compared to primes incongruent with the higher probability mask, as participants would be more inclined to respond in the biased mask direction.

5.3.1 Methods

5.3.1.1 Participants. Twelve right-handed university students (7 female, 5 male, mean age = 22.3 ± 3.8 years) participated in this study. All participants had normal or corrected-to-

normal visual acuity and were reimbursed for their involvement (\$20). Participants provided informed consent and the studies was conducted in accordance with the ethical guidelines set by the University of British Columbia.

5.3.1.2 Apparatus and Stimuli. The apparatus and stimuli were the same as Experiment 1. **5.3.1.3 Procedure.** The basic procedure was the same as Experiment 1, with the following exceptions. In order to examine the role of an intentional bias on unconscious processing, we manipulated the prime-mask sequence presented such that on 80% of trials a particular mask was displayed. Participants were made aware of this bias and instructed that on the majority of trials (80%) a left (or right) mask would appear. The direction of the mask bias was counterbalanced across participants, such that for half the participants a right mask appeared 80% of the time and for the other half, a left mask appeared 80% of the time. Participants completed one block of 150 trials.

5.3.1.4 Data Analysis. In order to examine the manipulation of response bias on performance across participants, we categorized data according to the mask displayed (high probability mask: presented on 80% of all trials vs. low probability mask: mask presented on 20% of all trials) and the relationship of the prime to the mask displayed (congruent, incongruent or neutral). Dependent variables were analyzed using a 2 Group (left mask displayed on 80% of all trials, right mask displayed on 80% of all trials) x 2 Mask (high probability, low probability) x 3 Prime Congruency (congruent, incongruent, neutral with respect to the mask) analysis of variance (ANOVA) with repeated measures on the last two factors. Because ANOVA did not reveal any significant interactions involving the group factor for any of the variables analyzed (p > 0.05), the results are discussed with reference to mask bias, as opposed to a specific mask direction.

5.3.2 Results

<u>Mask Reaction Time Task</u>. Mean correct reaction times (RT) are shown for both high and low probability responses as a function of prime congruency in Figure 2b. In comparing these results to performance in Experiment 1, it appears that RT was dependent on the mask displayed (i.e. high probability vs. low probability response required). ANOVA revealed that this was indeed the case. Participants were faster to make a response when the high probability mask was displayed compared to trials in which the low probability mask was

presented, F(1,10) = 30.832, p < 0.001. However, once the influence of response bias was accounted for, the primes influenced RT to the mask in a similar manner to Experiment 1 (Prime Congruency: F(2,20) = 95.692 < 0.001; Mask Displayed x Prime Congruency: F(2,20) < 1). This was confirmed by post hoc analyses which indicated that RT was significantly faster on congruent trials compared to neutral or incongruent trials, which also differed from each other. Given that the impact of the primes on performance was similar across response hands, we determined the mean congruency effect by taking the average difference in RT between congruent and incongruent trials. The average congruency effect was the same as Experiment 1 - 56 ms.

Similar to Experiment 1, we found that participants were very accurate in the <u>Mask</u> <u>Response Time</u> task (> 98% correct overall; the mean percentage of errors for each primemask combination displayed are provided in Table 2). However, in contrast to Experiment 1, ANOVA revealed that the percentage of errors was influenced by the mask displayed (F(1,10) = 12.993, p = 0.005), independent of prime-mask congruency (Prime Congruency: F(2,10) = 2.558, p = 0.103, Mask Displayed x Prime Congruency: (F(2,20) = 2.323, p = 0.124). Participants committed significantly more errors on trials in which the low probability mask was presented and they were to make the less probable response compared to trials in which the high probability mask was displayed.

<u>Prime Identification Task</u>. Mean accuracy collapsed across all prime-mask sequence combinations was $45.8\% \pm 10.7$ (SD), which did not differ from the chance level of 33% ($\chi^2 = 0.713$, p > 0.05).

5.3.3 Discussion

In the present experiment, we were interested in determining whether intentiondependent subliminal priming is sensitive to conscious response biases. To that end, we created a situation in which participants were able to intentionally favour a particular response. We then examined whether this intentional predisposition subsequently changed the impact of subliminally presented primes.

The manipulation of conscious response bias yielded the anticipated results and demonstrated that a higher probability event is responded to more quickly than an alternative,

less likely one (see LaBerge et al., 1969; Blackman, 1972; Hawkins et al., 1973; Heuer, 1982). Participants were faster to respond to the high probability mask compared to the low probability mask, even on trials in which a neutral prime was displayed. This selective predisposition for a particular response also created a tendency for participants to react slower and commit a greater number of errors on trials in which the less likely response was required. However, despite participants' predisposition to favour a response in the more probable direction, all primes (i.e. those indicating the same response as the high probability mask and those indicating the opposite response to the high probability mask), had an impact on performance. In fact, after accounting for the influence of response bias on performance (as demonstrated by changes in RT on neutral prime trials), results indicated that the magnitude of a prime's impact on action was similar to that observed in Experiment 1.

Thus, our results show clearly that if a stimulus is mapped to a response, it will influence performance, regardless of participants' intentional bias. In other words, participants cannot selectively modulate the impact of subliminal stimuli on performance when the unconscious information is within established stimulus-response mappings. These results extend current TDC accounts of subliminal processing, and suggest that the mapping of a stimulus to a particular response results in the automatic processing of task relevant information (i.e. primes within the established stimulus-response set will have a predictable influence on performance).

To explain how the impact of subliminal information on performance remained constant when an intentional response bias was imposed, we propose that participants began to prepare the more likely response prior to stimulus onset (see Miller, 1988 and Gehring et al. 1992). This advanced preparation pre-set the system to favour the more probable response at the time of prime presentation. In addition to explaining the RT results, this proposed advanced preparation explains why a higher proportion of errors were obtained on trials in which participants should have pressed the key associated with the less likely response. Furthermore, it does not preclude prime-related activity from having a similar influence on performance as observed in Experiment 1. We assume that the visuomotor system was adjusted to favour a particular response based on instructions provided. However, because left and right arrow primes were still relevant to the task at hand, the

stimuli were processed in a similar manner to Experiment 1 from the time of prime presentation onwards.

5.4 Experiment 3: The influence of an unconscious bias on subliminal processing

The results from the previous experiments suggest that if a stimulus is mapped to a particular response, unconscious events associated with a matching subliminal stimulus influence performance in an automatic manner. In the present experiment we continued to probe the conditional automaticity of subliminal processing proposed by TDC accounts by manipulating subliminal events. Like Experiment 1, participants were required to press left and right keys equally often. However, in contrast to Experiment 1, all primes were not displayed with equal probability. Specifically, one directional prime was presented on 80% of all trials. According to the TDC accounts of subliminal processing, the same pattern of results was expected to be observed in the present Experiment as in Experiment 1. Stimulus-response mappings would be established based on the instructions provided and given that participants intended to respond to left and right arrows equally often, we did not expect to observe a preference for a particular response.

5.4.1 Methods

5.4.1.1 Participants. Ten right-handed university students (6 female, 4 male, mean age = 23.9 ± 2.7 years) participated in this study. All participants had normal or corrected-to-normal visual acuity and were reimbursed for their involvement (\$20). Participants provided informed consent and the studies was conducted in accordance with the ethical guidelines set by the University of British Columbia.

5.4.1.2 Apparatus and Stimuli. The apparatus and stimuli were the same as Experiment 1. **5.4.1.3 Procedure.** The basic procedure was the same as Experiment 1, with the following exception. To examine the role of an unconscious bias on subliminal processing, a specific directional prime (left or right) was displayed on the majority of trials (biased prime displayed on 80% of all trials). Similar to Experiment 1, left and right mask arrows were presented on an equal number of trials. Participants completed 5 blocks of 120 trials. **5.4.1.4 Data Analysis.** Figure 3 tracks changes in RT for congruent and incongruent trials when the high probability prime was displayed. Figure 3 shows that performance was quickly modified in response to the manipulation of prime bias. To allow for the initial adjustment in performance, data from the first experimental block were excluded from analyses. For the remaining trials, we categorized data according to the relationship of the mask to the high probability prime (mask indicated the same response as the high probability prime or opposite response). Data within these categories were then separated according to the relationship of the mask (congruent, incongruent or neutral).

Dependent variables were analyzed using a 2 Group (left prime displayed on the majority of trials, right prime displayed on the majority of trials) x 2 Mask (same response as the (biased) high probability prime, opposite response to the high probability prime) x 3 Prime Congruency (congruent, incongruent, neutral with respect to the mask) analysis of variance (ANOVA), with repeated measures on the last two factors. ANOVA did not reveal any significant interactions involving the group factor for any of the variables analyzed (p > 0.05). Thus, the results are discussed with reference to the relationship of the mask to the biased prime, as opposed to a specific mask direction.

5.4.2 Results

<u>Mask Reaction Time Task</u>. Figure 2c displays mean correct reaction times (RT) for both masks (mask indicating the same response as the high probability prime and mask indicating the opposite response to the high probability prime) as a function of prime congruency. Surprisingly, the pattern of results differs from Experiment 1. Participants appear to have been faster on trials in which the mask incongruent with the high probability prime was displayed. This observation was consistent with the ANOVA, which revealed a significant main effect for mask, F(1,8) = 21.113, p = 0.002. However, like Experiment 2, once participants' tendency to respond faster in a particular direction was taken into account, the impact of primes on performance was similar to Experiment 1 (Prime Congruency: F(2,16) = 50.896, p < 0.001, Mask x Prime Congruency: F(2,16) = 1.397, p = 0.276). Specifically, post hoc analyses indicated that RT was significantly faster on congruent trials than either neutral or incongruent trials and RT was significantly slower on incongruent trials compared to neutral trials. The average congruency score was obtained in a similar manner to E1 and E2

(i.e. mean RT for all incongruent trials minus mean RT for all congruent trials). The average difference in RT between congruent and incongruent trials was approximately 50 ms, which did not differ from Experiments 1 or 2 (One-way ANOVA: F(2,31) < 1). The congruency scores for all experiments are displayed in Figure 2e.

Participants were very accurate in the <u>Mask Reaction Time</u> task (> 98% correct overall; the mean percentage of errors for each prime-mask combination displayed are provided in Table 2). On trials in which participants made an error, ANOVA revealed significant main effects (Mask: F(1,8) = 7.735, p = 0.02; Prime Congruency: F(2,16) =7.612, p = 0.005). The interaction was not significant, F(2,16) = 1.711, p = 0.212. Post hoc analyses indicated that participants made significantly more errors on trials in which the mask congruent with the high probability prime was displayed compared to trials in which the mask incongruent with the high probability primes was displayed. As well, participants completed more errors on incongruent prime-mask trials compared to congruent or neutral prime-mask combinations.

<u>Prime Identification task</u>. Mean accuracy collapsed across all prime-mask sequence combinations was $45.1\% \pm 9.3$ (SD), which did not differ from the chance level of 33% ($\chi^2 = 0.630$, p > 0.05).

5.4.3 Discussion

In the present experiment we biased the prime displayed and hence manipulated an unconscious event. Results obtained in Experiments 1 and 2 indicated that unconscious processes applied to task relevant subliminal stimuli influenced action in an automatic manner. Specifically, whatever processes were applied to one stimulus within an established stimulus-response mapping, were also applied to the other (i.e. the impact of subliminal information on action could not be selectively modulated). On this basis we hypothesized that manipulating the prime displayed, while instructing participants that left and right mask arrows were equally probable, would not affect the degree to which subliminal primes influenced performance. As expected, we found that both directional primes had a similar impact on performance (50 ms mean congruency effect), which did not differ from Experiments 1 or 2. These results provide further support for the relative automaticity of subliminal processing once intentional stimulus-response mappings are established. Again, after a stimulus is mapped to a particular response, the impact of task relevant subliminal stimuli on performance cannot be changed selectively. Our manipulation of prime probability did not lead to any differences in the degree to which the primes (the high probability versus the low probability prime) affected performance. However, this manipulation of events that were outside of participants conscious awareness did have one important effect. Specifically, biasing the frequency of the prime led to adjustments in the visuomotor system. Similar to Experiment 2, we found that participants modified their response tendencies such that one response was "favoured" over the other. In this instance, as reflected by both the RT data and error results, participants were more inclined to initiate a response to the mask incongruent with the high probability prime. For example, even on trials in which the neutral prime was followed by the mask incongruent with the high probability prime compared to trials in which the mask congruent with the high probability prime was displayed.

In order to explain the results obtained in Experiment 2, we proposed that participants consciously adjusted the visuomotor system in order to favour the activation of the response associated with the high probability mask. While this selective predisposition for a particular response resulted in differences in RT between the two responses, it did not modulate the impact of the subliminal primes. Results from the current experiment, suggest that once again the visuomotor system was modified (such that participants were more inclined to initiate a particular response), as a result of a directional bias. However, in this instance, the adjustments in the visuomotor system resulted from the biasing of an unconscious event (i.e. the biasing of the prime displayed). Thus, these findings indicate that subliminal events are not restricted to activating a corresponding response.

5.5 Experiment 4: The influence of the relationship between conscious and unconscious events on subliminal processing

In Experiments 2 and 3, we manipulated either a conscious or unconscious event by biasing the mask or prime displayed. These events were manipulated independently of each other, such that on 50% of all trials in which directional primes were displayed, the prime and mask were congruent. However, biasing either the mask or prime did shift the relationship between conscious and unconscious events indirectly. For example, in Experiment 2 (manipulation of mask probability), while directional primes were followed by a congruent mask on 50% of the trials overall, the ability of a specific directional prime to indicate the upcoming response depended on its relationship to the biased mask. When the prime pointing in the same direction as the high probability mask was displayed, it was most often followed by a congruent mask. In contrast, when a prime pointing in the opposite direction of the high probability mask was displayed, it was followed by an incongruent mask on the majority of trials.

In contrast to Experiment 2, both directional primes were followed by a congruent mask 50% of the time in Experiment 3 (manipulation of prime probability). However, because one prime was displayed more often than the other, the ability of a specific directional prime to accurately predict the required response with respect to the number of trials completed overall, depended on the prime's identity. For example, on trials in which the high probability prime was displayed it was followed by a congruent mask on 40% of all trials, whereas when the low probability prime was displayed it was followed by a congruent mask on only 5% of all trials. Furthermore, the high probability prime was followed by an incongruent mask on 40% of all trials and the low probability prime preceded an incongruent mask on 5% of all trials. Based on these independent manipulations of a conscious or unconscious event we found that response patterns could be modified in general, such that one response was favoured over the other. However, all subliminal stimuli within the established stimulus-response mapping had a similar impact on performance (i.e. the magnitude of the priming effect remained constant as measured by a congruency score).

In the present experiment we examined if the priming effect observed in the previous experiments would be modulated when the relationship between the conscious and

unconscious events was manipulated directly. In order to investigate the interaction between conscious and unconscious events we changed the proportion of congruent trials displayed. Participants completed three blocks of trials; one in which the prime and mask were congruent on 80% of all trials, another when the prime and mask were congruent on 50% of all trials and a third block in which only 20% of the trials were congruent.

Based on the results of Experiment 3, it is evident that response patterns can be modified as a result of unconscious events. But this modification in performance appears to be restricted to shifting response tendencies, such that one response is favoured over the other. In the present experiment both left and right primes, as well as left and right masks, were displayed with equal probability. Thus, we did not expect to observe a shift in response tendencies such that one response was favoured over the other. Furthermore, based on current TDC accounts of subliminal processing, we hypothesized that the same overall congruency effect obtained in Experiments 1 through 3 would be observed in the present experiment regardless of the proportion of congruent trials displayed.

5.5.1 Methods

5.5.1.1 Participants. Twenty-four right-handed university students (13 female, 11 male, mean age = 23.8 ± 5.8 years) participated in this study. All participants had normal or corrected-to-normal visual acuity and were reimbursed for their involvement (\$20). Participants provided informed consent and the studies was conducted in accordance with the ethical guidelines set by the University of British Columbia.

5.5.1.2 Apparatus and Stimuli. The apparatus and stimuli were the same as Experiment 1, except that neutral primes were not displayed in the <u>Mask Reaction Time</u> task or in the <u>Prime</u> <u>Identification</u> task.

5.5.1.3 Procedure. The basic procedure was the same as Experiment 1, with the following exception. In order to examine the relationship between the conscious and unconscious events the proportion of trials in which the prime and mask were congruent varied between experimental blocks (80%, 50% or 20% congruent). Similar to Experiment 1, in all blocks, left and right primes, as well as left and right masks were displayed on an equal number of trials. Participants completed the 3 blocks of 240 trials in a random order.

5.5.1.4 Data Analysis. The first 80 trials of each experimental block were excluded from analyses in order to provide participants with the opportunity to adapt to the proportion of congruent trials displayed. In order to display the results, we collapsed performance across right and left responses.

5.5.2 Results

<u>Mask Response Time Task</u>. Mean correct reaction times (RT) for congruent and incongruent trials are displayed as a function of probability distribution in Figure 2d. In this figure we observe a separation in response patterns depending on the proportion of congruent trials displayed. For example, the slowest mean RT was obtained on incongruent trials in the experimental block in which the proportion of congruent trials was 80%, while the fastest mean RT was obtained on congruent trials in the same experimental block. This suggests that the ability of subliminal events to correctly predict the upcoming response influenced the impact of the primes on performance (e.g. affected RT on both congruent and incongruent trials).

Consistent with our observations, a 3 Probability Distribution (80%, 50%, 20% congruent trials) x 2 Mask (left, right) x 3 Prime Congruency (congruent, incongruent with respect to the mask) repeated measures analysis of variance (ANOVA) revealed a significant interaction between probability distribution and prime congruency (F(2,46) = 6.931, p = 0.002). Significant main effects were also observed for mask (F(1,23) = 9.323, p = 0.006) and prime congruency (F(1,23) = 429.895, p < 0.001). However, even though participants were slightly faster to complete responses made to the right compared to the left, the influence of the proportion of congruent trials and prime congruency on performance was independent of the mask displayed (Probability Distribution x Mask: F(2,46) < 1, Mask x Prime Congruency: F(1,23) = 1.379, p = 0.252, Probability Distribution x Mask x Prime Congruency: F(2,46) = 1.029, p = 0.365).

Thus, to examine the difference in the magnitude of the priming effect between different blocks of trials, we collapsed performance across right and left responses and determined the difference in RT between congruent and incongruent trials (congruency effect) for each experimental block. A 3 Probability Distribution (80%, 50%, 20%) repeated measures ANOVA revealed a significant main effect, F(2,46) = 6.931, p = 0.002. The

primes had a greater impact on performance, as indicated by a larger congruency score, in the block of trials in which 80% of the trials were congruent ($\bar{x} = 52.9 \text{ ms} \pm 15.2 \text{ SD}$) compared to when only 20% of the trials were congruent ($\bar{x} = 40.7 \text{ ms} \pm 15.8 \text{ SD}$).

Participants were correct on approximately 97% of all trials (Table 2 provides the mean percentage of errors for each prime-mask combination displayed). On trials in which participants made an error, a 3 Probability Distribution (80%, 50%, 20% congruent trials) x 2 Mask (left, right) x 3 Prime Congruency (congruent, incongruent with respect to the mask) repeated measures analysis of variance revealed differences depending on the probability distribution and prime congruency (Probability Distribution: F(2,46) = 7.947, p < 0.001, Prime Congruency: F(1,23) = 35.751, p < 0.001, Probability Distribution x Prime Congruency: F(2,46) = 5.785, p = 0.006). Specifically, participants made the most errors on incongruent trials in the experimental block in which the prime and mask were congruent 80% of the time. There was no difference in the number of errors completed on trials in which the prime and mask were congruent, regardless of probability distribution. Furthermore, the number of errors was independent of the mask displayed (Mask: F(1,23) = 2.439, p = 0.132).

<u>Prime Identification Task</u>. Chance performance in this task was 50% (given that directional primes were displayed with equal probability). Mean accuracy collapsed across all prime-mask sequence combinations was 55.1% \pm 9.7 (SD). This performance did not differ significantly from the chance level of 50% at the p = .05 level ($\chi^2 = 0.250$).

5.5.3 Discussion

In the present experiment we examined the influence of the relationship between conscious and unconscious events on subliminal priming by varying the proportion of congruent trials. In accordance with TDC accounts of subliminal processing and our previous results, both left and right directional primes had a similar impact on performance (i.e. there was no selective processing of a particular prime for action). However, in contrast to our previous results, the overall impact of the primes was modulated depending on the proportion of congruent trials. Results indicated that while the typical pattern of performance was maintained across experimental blocks (i.e. faster responses on congruent trials and

slower responses on incongruent trials), the magnitude of the impact of the primes on action differed depending on the proportion of congruent trials displayed. For example, the primes had the greatest influence on performance, as measured by congruency scores, when they accurately predicted the upcoming response on the majority of trials (80% congruency block). Furthermore, errors completed on incongruent trials suggested that participants were more willing to commit to the response indicated by the prime when the proportion of congruent trials was 80% compared to when the prime and mask were congruent on only 50% or 20% of all trials.

In agreement with our results, Jaskowski and colleagues (2003) have recently demonstrated that manipulating the proportion of congruent trials in a metacontrast masking RT task in which pairs of stimuli are displayed in rapid succession, leads to differences in response patterns. In the study by Jaskowski et al. (2003), pairs of stimuli were displayed, such that one stimulus was presented to the left of fixation and the other to the right of fixation. The target was designated according to shape and participants were instructed to respond to the spatial location of the target (left or right) as quickly and accurately as possible. In different blocks of trials, the target was preceded by a series of primes which correctly indicated its location on 80% or 20% of all trials. In accordance with our results, Jaskowski et al. (2003) found that the primes had the greatest impact on performance when they accurately predicted the upcoming response on 80% of all trials. Thus, these results, combined with the results obtained in the present experiment, suggest that subliminal processing is not restricted to activating a corresponding response. As a consequence of manipulating the relationship between conscious and unconscious events, the system adjusts to allow subliminal information to have more or less control over performance.

5.6 General Discussion

The goal of the current research was to investigate the intention-dependent automaticity of the unconscious system as proposed by current top-down contingency accounts of subliminal processing (i.e. Direct Parameter Specification, DPS (Neumann, 1990), and the Action Trigger Hypothesis (Kunde et al., 2003)). To address this issue we used a metacontrast masking paradigm and manipulated the stimulus events displayed, either at a conscious or an unconscious level. Experiment 1 established the impact of subliminal primes on responses to the mask stimuli when the prime-mask sequence was displayed in a typical metacontrast masking RT task. Hence, results obtained in this task were used as a comparison in order to evaluate possible changes in performance due to experimental manipulations.

In Experiment 2, we manipulated participants' expectations (i.e. intentions) regarding the upcoming response by instructing participants that a particular directional mask would appear on the majority of trials. In Experiment 3 we manipulated an unconscious event by biasing a particular directional prime, such that it was displayed on the majority of trials. Finally, in Experiment 4, we changed the relationship between conscious and unconscious events by altering the proportion of trials in which the prime and mask were congruent.

According to current TDC-based accounts, the processing of subliminal information for action is automatic, provided that the incoming sensory information is within an established stimulus-response mapping. For example, these theories (i.e., DPS and Action Triggering) propose that based on instructions provided, a consciously mediated control mechanism maps a particular stimulus to a particular response. This mapping creates release conditions or "action-triggers" (as described by Kunde and colleagues (2003)). Thus, when the incoming stimulus is within the established stimulus-response mapping, the corresponding action-trigger is automatically activated, resulting in an immediate and predetermined influence on action (Neumann, 1990; Ansorge et al., 2002; Kunde et al., 2003).

In agreement with TDC accounts of subliminal processing, we found that regardless of experimental manipulation, responses were initiated earlier on trials in which the prime and mask were congruent compared to incongruent trials. Furthermore, in all four experiments, left and right directional primes had a similar influence on performance. For example, even in Experiment 2, in which participants were instructed that a particular response would be required on the majority of trials, left and right directional primes influenced responses to the same degree. Thus, it appears that in a metacontrast masking RT task in which two stimuli are mapped to two response alternatives, one cannot selectively modulate the impact of (or differentially process) the subliminal stimuli.

However, in contrast to the current TDC framework, our results indicate that unconscious processing is not restricted to activating a corresponding response. Results from Experiments 2, 3 and 4 suggest that while the impact of a specific subliminal stimulus cannot

be selectively modulated, performance patterns in general (i.e. the visuomotor system) can be adjusted in response to manipulations of conscious and/or unconscious events. In particular, we found that visuomotor processing was modified in Experiments 2 (manipulation of a conscious event) and 3 (manipulation of an unconscious event), such that responses to a particular mask were initiated faster than the alternative response. In Experiment 2, this was reflected by participants being faster to initiate a response in the direction of the high probability mask, whereas in Experiment 3, participants were faster to initiate responses in the direction of the mask incongruent with the high probability prime. In addition to modulations in response tendencies, results from Experiment 4 indicate that the impact of subliminal stimuli on action can be modified in response to changes in the relationship between conscious and unconscious events. For example, when the prime accurately predicted the upcoming response on the majority of trials it had a greater effect on performance compared to when it was followed by an incongruent mask on the majority of trials.

In attempt to explain how the visuomotor system may be modulated as a result of varying the proportion of congruent prime-mask trials displayed, Jaskowski and colleagues (Jaskowski et al., 2003; Wolbers et al., 2006) have recently suggested that participants strategically adapt their performance by monitoring overt error frequency. According to Jaskowski, participants recognize the goal of the task is to react as quickly as possible but they also want to keep errors to a minimum. In experiments manipulating the proportion of congruent trials, participants are at a greater risk of making an error when performing the task under conditions in which the prime and mask are congruent on 20% of the time, compared to when the prime and mask are congruent on 80% of all trials. Thus, by monitoring error performance, Jaskowski and colleagues (2003) propose that participants quickly adjust visuomotor processes according to task restrictions in order to ensure that they react as quickly as possible while maintaining a low number of errors. In the instance when the proportion of congruent trials is 80%, these adjustments allow for information from the prime to be readily carried to motor areas where it activates its corresponding response. In contrast, when only 20% of the trials are congruent, subliminal information is not allowed to influence motor processes to as great an extent.

The results of our Experiment 4 in which we varied the proportion of congruent trials are in agreement with the results obtained by Jaskowski and colleagues (Jaskowski et al., 2003; Wolbers et al., 2006). The primes had a greater influence on performance when they accurately predicted the upcoming response on the majority of trials. While the modulation of the visuomotor system to allow the primes to have more or less of an impact on performance was to participants' benefit (e.g. allowed for faster RT while ensuring that responses were correct), we are hesitant to refer to this modification as strategic. It is unlikely that adjustments in the ability of subliminal information to influence action arose as a result of monitoring overt error performance in our experiments. The average number of errors made by our participants was much lower than in the studies by Jaskowski and colleagues (< 3% overall vs. approximately 10%). In addition, the modulation of the visuomotor system observed in Experiment 3 as a result of manipulating an unconscious event, while maintaining overt performance at baseline conditions, suggests that the monitoring of overt error frequency is not a prerequisite for shifts in the visuomotor system. Finally, combining the results of Experiments 3 and 4, it appears that the visuomotor system can be adjusted after a relatively small number of trials (i.e. < 80). Thus, we propose that one does not need to be consciously aware of performance in order to modulate visuomotor processing.

At present we can only speculate how modifications in the visuomotor system arose as a result of manipulating unconscious events. We propose that the visuomotor system is subject to modulation by inhibitory signals arising as a result of subliminal conflicts. These inhibitory signals accumulate over time as a result of response competition arising between prime and mask-related motor activation. In Experiment 4, the system would be subject to higher levels of inhibition when the proportion of congruent trials displayed was 20% compared to when the proportion of congruent trials was 80%. Increased levels of inhibition would lead to a general dampening of the system such that prime-related activity could not contribute to a response as it would when 80% of the trials were congruent and less inhibitory activity occurred. In Experiment 3, prime-related activity would have to be inhibited on a greater number of trials in which the high probability prime was displayed compared to when the low probability prime was presented. In contrast to Experiment 4, these inhibitory signals would be specific to a particular response and thus, lead to a

reduction in the activation level of the response associated with the high probability prime compared to the response associated with the low probability prime.

In Experiment 2 (manipulation of a conscious event), we assumed that adjustments in the visuomotor system arose as the result of participants consciously adjusting the level of readiness (or activity) of the more likely response. However, given the proposal discussed above, we would also predict that conflict arising between subliminal events may have influenced performance. The prime pointing in the opposite direction of the high probability response was followed by an incongruent mask more often than the prime pointing in the same direction as the bias. Thus, more inhibitory signals would be associated with the response in the opposite direction to the bias, possibly contributing to participants' tendency to respond faster in the high probability direction compared to the low probability direction.

5.7 Conclusion

Our results indicate that participants cannot selectively modulate the impact of task relevant subliminal information on action. Thus, in accordance with TDC accounts of subliminal processing, we found that all subliminal stimuli within an established stimulus-response set had an equivalent impact on performance. However, in contrast to the proposed limits of unconscious processing put forth by the current TDC framework, we have demonstrated that the visuomotor system can be modulated in response to manipulations in stimulus events occurring outside of conscious awareness. For example, our results indicate that (1) response tendencies can be varied such that participants are more inclined to initiate a particular response as a result of an unconscious manipulation and (2) the overall ability of subliminal stimuli to influence action can be modified when the relationship between consciously and unconsciously triggered events is varied.

5.8 Tables

Table 5.1. Total number of trials completed per prime-mask combination within each of the four experiments. The first word (i.e. neutral, congruent, incongruent) indicates the relationship of the prime with the subsequent mask. In Experiment 2, masks are designated as high probability mask (displayed on 80% of all trials) or low probability mask (displayed on 20% of all trials). In Experiment 3, masks are designated as congruent with high probability prime (pointed in the same direction as the biased prime) or incongruent with high probability prime (pointed in the opposite direction to the biased prime). In Experiment 4, the number of trials are provided for each experimental block (80% = 80% of all trials congruent).

Experiment 1	Neutral - Left Mask	Neutral - Right Mask	Congruent – Left Mask	Congruent – Right Mask	Incongruent – Left Mask	Incongruent – Right Mask
	20	20	20	20	20	20
Experiment 2	Neutral – High Probability Mask	Neutral – Low Probability Mask	Congruent – High Probability Mask	Congruent – Low Probability Mask	Incongruent – High Probability Mask	Incongruent – Low Probability Mask
	40	10	40	10	40	10
Experiment 3	Neutral – Mask congruent with high probability prime	Neutral – Mask incongruent with high probability prime	Congruent – Mask congruent with high probability prime	Congruent – Mask incongruent with high probability prime	Incongruent – Mask congruent with high probability prime	Incongruent – Mask incongruent with high probability prime
	30	30	240	30	30	240
Experiment 4			Congruent – Left Mask	Congruent – Right Mask	Incongruent – Left Mask	Incongruent – Right Mask
80%			96	96	24	24
50%			60	60	60	60
20%			24	24	96	96

Table 5.2. Mean RT (SE) in ms and mean percentage of errors completed (SE) per primemask combination for each of the four experiments. The first word (i.e. neutral, congruent, incongruent) indicates the relationship of the prime with the subsequent mask. In Experiment 2, masks are designated as high probability mask (displayed on 80% of all trials) or low probability mask (displayed on 20% of all trials). In Experiment 3, masks are designated as congruent with high probability prime (pointed in the same direction as the biased prime) or incongruent with high probability prime (pointed in the opposite direction to the biased prime). In Experiment 4, results are provided for each experimental block (80% = 80% of all trials congruent).

Experiment 1	Neutral - Left Mask	Neutral - Right Mask	Congruent – Left Mask	Congruent – Right Mask	Incongruent – Left Mask	Incongruent – Right Mask
Reaction time	345 (11)	351 (7)	331 (10)	333 (7)	389 (9)	388 (8)
Errors	1.0 (0.7)	1.0 (0.7)	1.5 (0.8)	1.0 (0.7)	6.5 (2.0)	9.0 (1.9)
Experiment 2	Neutral – High Probability Mask	Neutral – Low Probability Mask	Congruent – High Probability Mask	Congruent – Low Probability Mask	Incongruent – High Probability Mask	Incongruent – Low Probability Mask
Reaction time	345 (13)	396 (12)	327 (10)	378 (15)	386 (10)	432 (12)
Errors	0 (0)	6.7 (1.9)	0 (0)	2.5 (1.8)	0.6 (0.4)	10.0 (3.7)
Experiment 3	Neutral – Mask congruent with high probability prime	Neutral – Mask incongruent with high probability prime	Congruent – Mask congruent with high probability prime	Congruent – Mask incongruent with high probability prime	Incongruent – Mask congruent with high probability prime	Incongruent – Mask incongruent with high probability prime
Reaction time	358 (13)	341 (17)	335 (14)	317 (13)	390 (13)	362 (12)
Errors	0.6 (0.5)	0.2 (0.2)	0.1 (0.04)	0.1 (0.1)	1.7 (0.7)	0.7 (0.4)
Experiment 4			Congruent – Left Mask	Congruent – Right Mask	Incongruent – Left Mask	Incongruent – Right Mask
80% - RT			360 (9)	353 (9)	405 (9)	415 (9)
80% - Errors			1.3 (0.4)	0.4 (0.2)	9.1 (1.7)	6.0 (1.4)
50% - RT			366 (10)	353 (8)	400 (8)	412 (9)
50% - Errors			0.6 (0.3)	0.7 (0.3)	5.6 (1.0)	3.1 (0.8)
20% - RT			367 (9)	358 (9)	397 (8)	409 (8)
20% - Errors			0.8 (0.4)	1.0 (0.6)	2.9 (0.9)	3.0 (0.8)

5.9 Figures

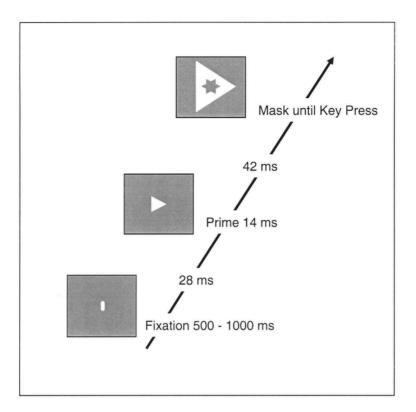
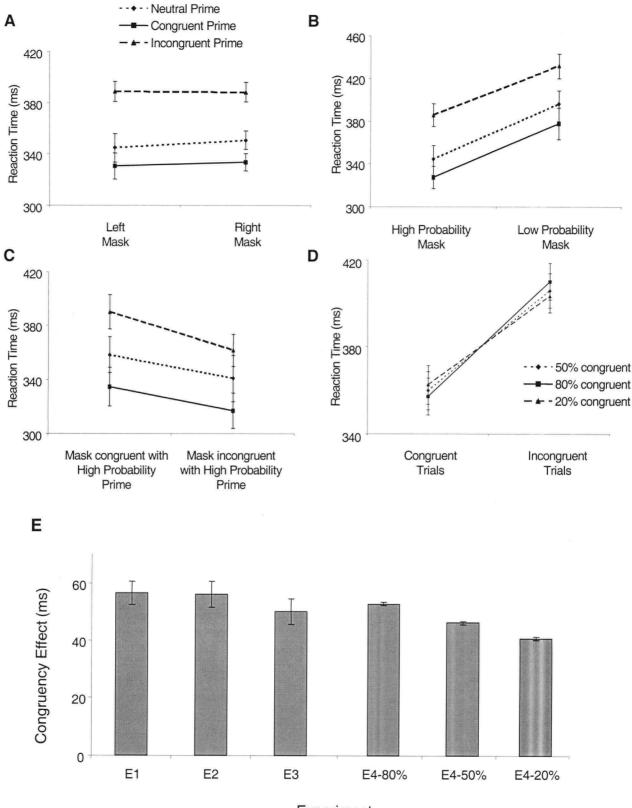


Figure 5.1. Temporal sequence of a typical experimental trial. Left and right arrows, as well as a neutral stimulus, served as primes. Participants were instructed to make a response based on the direction of the mask arrow (e.g. press a left key in response to a left arrow mask and press a right key in response to a right arrow mask).

Figure 5.2. Choice reaction times (RT) to the mask stimuli as a function of prime congruency (congruent (denoted by a square symbol), incongruent (triangle) or neutral (diamond) with respect to the mask displayed). (A) Experiment 1: Results are shown for left and responses. (B) Experiment 2: Results are displayed according to the mask presented (high probability mask: mask displayed on 80% of all trials, low probability mask: mask displayed on 20% of all trials) (C): Experiment 3: Results are displayed according to the mask's relationship with the high probability prime (congruent: mask indicated the same response as the high probability prime vs. incongruent: mask indicated the opposite response to the high probability prime). (D) Experiment 4: Results are shown for congruent and incongruent trials as a function of the proportion of congruent prime-mask trials displayed within an experimental block (80% (square), 50% (diamond), or 20% (triangle)). (E) The overall priming effect (congruency score) obtained in each of the four experiments (E1 =Experiment 1, etc.). In Experiment 4, results are provided for each of the three experimental blocks in which the proportion of congruent prime-mask trials varied (80%, 50%, or 20% congruent). The congruency score was calculated as the difference in mean RT between incongruent and congruent prime-mask trials. Error bars denote standard errors.



Experiment

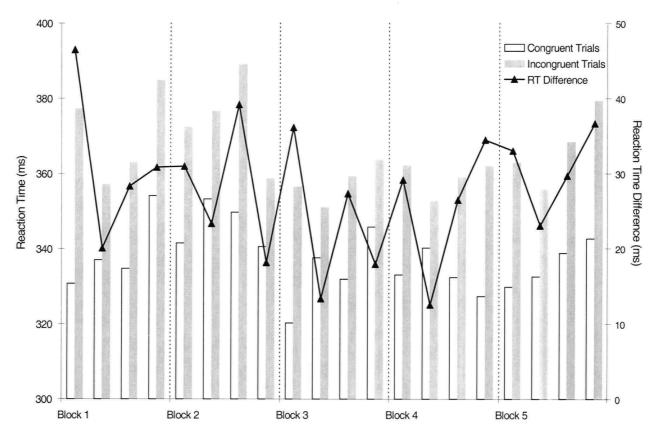


Figure 5.3. Data from Experiment 3, on trials in which the high probability prime was displayed. Each bar represents the mean reaction time (RT) obtained on 10 *consecutive* congruent or incongruent prime-mask trials (primary y-axis). The solid black line indicates the difference between the two RT scores. The corresponding values are provided on the secondary y-axis. Note: (1) in order to calculate these mean RT scores, trials in which participants pressed the correct key were first separated according to prime-mask congruency (i.e. congruent or incongruent trials in which the high probability prime was displayed) within each experimental block. The first 10 trials within these categories were then averaged together, then the second 10, etc. Due to the fact that participants performed a number of errors and only 48 trials were displayed per each condition, mean RT are provided for only four groups of 10 consecutive trials within each experimental block.

5.10 References

- Ansorge, U. (2004). Top-down contingencies of nonconscious priming revealed by dualtask interference. *The Quarterly Journal of Experimental Psychology*, 2004, 1123-1148.
- Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-545.
- Ansorge, U., & Neumann, O. (2005). Intentions determine the effect of invisible metacontrast-masked primes: Evidence for top-down contingencies in a peripheral cuing task. Journal of Experimental Psychology: Human Perception and Performance, 31, 762-777.
- Bertelson, P., & Barzeele, J. (1965). Interaction of time uncertainty and relative signal frequency in determining choice reaction time. *Journal of Experimental Psychology*, 70, 448-451.
- Blackman, A.R. (1972). Influence of stimulus and response probability on decision and movement latency in a discrete choice reaction task. *Journal of Experimental Psychology*, 92, 128-133.
- Bodner, G.E., & Dypvik, A.T. (2005). Masked priming of number judgments depends on prime validity and task. *Memory and Cognition*, 33, 29-47.
- Bodner, G.E. Mason, M.E.J. (2001). Prime validity affects masked repetition priming:
 Evidence for an episodic resource account. *Journal of Memory and Language*, 45, 616-647.
- Bodner, G.E. Mason, M.E.J. (2003). Beyond spreading activation: An influence of relatedness proportion on masked semantic priming. *Psychonomic Bulletin & Review*, 10, 645-652.

Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.

- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1595.
- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P.-F., & Le Bihan, D. (1998). Imaging unconscious

semantic priming. Nature, 395, 597-600.

- Enns, J.T., & DiLollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Enns, J.T., & Oriet, C. (2007). Visual similarity in masking and priming: The critical role of task relevance. *Advances in Cognitive Psychology*, in press.
- Gehring, W.J., Gratton, G., Coles, M.G.H., & Donchin, E. (1992). Probability effects on stimulus evaluation and response processes. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 198-216.
- Hawkins, H.L., MacKay, S., Holley, S., Friedin, B., & Cohen, S. (1973). Locus of the relative frequency effect in choice reaction time. *Journal of Experimental Psychology*, 101, 90-99.
- Heuer, R.H. (1982). Choice between finger movements of different and identical form: The effect of relative signal frequency. *Psychological Research*, 44, 323-342.
- Jaskowski, P., Skalska, B., Verleger, R. (2003). How the self controls its "automatic pilot" when processing subliminal information. *Journal of Cognitive Neuroscience*, 15, 911-920.
- Kahneman, D. (1968). Methods, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70, 404-425.
- Kiesel, A., Kunde, W., & Hoffmann, J. (in press). Mechanisms of subliminal response priming. *Advances in Cognitive Psychology*.
- Kunde, W., Kiesel., A., & Hoffmann, J. (2003) Conscious control over the content of unconscious cognition. *Cognition*, 10, 198-205.
- LaBerge, K., Legrand, R., & Hobbie, R.K. (1969). Functional identification of perceptual and response biases in choice reaction time. *Journal of Experimental Psychology*, 79, 295-299.
- Laming, D.R.J. (1969). Subjective probability in choice-reaction time experiments. *Journal* of Mathematical Psychology, 6, 81-120.
- Miller, J. (1998). Effects of stimulus-response probability on choice reaction time: Evidence from the lateralized readiness potential. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1521-1535.

- Naccache, L., & Dehaene, S. (2001). Unconscious semantic priming extends to novel unseen stimuli. *Cognition*, 80, 223-237.
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-215.
- Neumann, O., & Klotz, w. (1994). Motor responses to nonreportable, masked stimuli: Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. Proceedings of the National Academy of Sciences of the United States of America, 100, 6275-6280.
- Wolbers, T., Eszter, D.S., Verleger, R., Kraft, S., McNamara, A., Jaskowski, P., & Buchel,
 C. (2006) Changes in connectivity profiles as a mechanism for strategic control over interfering subliminal information. *Cerebral Cortex*, 16, 857-865.

CHAPTER 6 GENERAL DISCUSSION

The goal of the present research was to examine the properties of visuomotor processing occurring in the absence of conscious awareness. Specifically, I wished to investigate the extent to which subliminal processes could influence motor performance. In order to examine unconscious visuomotor processing I presented stimuli through the psychophysical procedure of metacontrast masking. Metacontrast masking is a form of backward masking in which the visibility of a briefly displayed visual stimulus (the *prime*) is greatly reduced when it is followed by a second visual stimulus (the *mask*) that closely fits around the outer contours of the prime but does not touch it. Because the prime fails to be processed up to the level of conscious awareness as a result of metacontrast masking, it is assumed that one does not gain conscious access to the relationship between information provided by the prime and the imperative mask stimulus (Jaskowski et al., 2003). Thus, in research employing metacontrast masking procedures, any influence the prime has on performance arises as a result of unconscious visuomotor processing, enabling one to examine the extent to which processing of unconscious information can contribute to motor behaviour.

Two of the main findings from this research include: (1) unconscious visuomotor processing can result in the modification of an overt response, such that a goal-directed movement is adjusted in response to a subliminal stimulus and (2) the visuomotor system can be modified in response to unconscious events. In this chapter I will outline how these findings fit with current theories (and models) of subliminal visuomotor processing and outline two possible mechanisms for how subliminal stimuli influence action. Within both visuomotor processing mechanisms put forth, I propose that the influence of a subliminal stimulus on action is dictated by task constraints. However, before discussing my results I will first briefly assert that metacontrast masking did indeed prevent participants from gaining conscious access to the presence of the prime stimuli.

6.1 Perceptual identification

At the end of each experimental session, participants were questioned on the stimulus sequence displayed and asked to perform a <u>Prime Identification</u> task. In response to questions regarding the stimulus sequence displayed, all participants reported the presence of a single large arrow. Furthermore, no participant spontaneously reported *seeing* a prime stimulus and when asked specifically to identify the primes in the <u>Prime Identification</u> task, participants indicated they were merely guessing. These subjective reports were validated by participants' overall poor performance in the <u>Prime Identification</u> task. In general, perceptual reports revealed that participants were unable to consciously identify the primes displayed. Given that participants incorrectly reported the prime's identify on the majority of trials in a <u>Prime Identification</u> task, in which they were explicitly aware of the presence of the primes and could focus all of their attention on attempting to identify which prime had been presented, I am confident that any influence of the primes on performance arose as a result of subliminal visuomotor processing.

6.2 Current explanations of the masked priming phenomenon

6.2.1 Metacontrast masking

While the focus of the current research is on the ability of subliminal stimuli to influence action, it is important to note possible mechanisms for how (or why) a prime is masked from conscious awareness, as associated processes will also be unavailable to guide action. In the introduction (Section 1.3) I outlined the cortical re-entrant explanation of metacontrast masking (Di Lollo et al., 2000; Enns and Di Lollo, 2000). According to Di Lollo and colleagues' cortical re-entrant processing model, conscious awareness arises when there is a match between a descending code (representing a perceptual hypothesis) and ongoing activity in lower visual areas. Thus, a prime is rendered "invisible" to the conscious system as a result of the mask evoking a new pattern of stimulation in the primary visual cortex, which does not match the cortical re-entrant processes signalling prime-related information.

A second explanation put forth to explain why a prime is masked from awareness by metacontrast is the dual-channel, sustained-transient view. According to the standard twochannel view, a prime is rendered invisible as a result of mask-evoked activity entering the nervous system later in time (Weistein, 1975; Breitmeyer, 1984). For example, the dualchannel, sustained-transient approach to visual information processing suggests that the onset of a stimulus results in the initiation of neural activity in two channels. In particular, activity is simultaneously evoked in a sustained channel, involved in the relatively slow processing of object features (i.e. brightness, colour, edges and figural details), and a transient channel, involved in fast, coarse pattern processing which signals the spatial location or the change of spatial location (motion) of a stimulus (Breitmeyer and Ganz, 1976; Breitmeyer and Ogmen, 2000). Thus, the two-channel view posits that the prime is masked by metacontrast due to transient activity evoked in response to the mask stimulus which terminates processing of the prime in the sustained channel at an early, pre-categorical level.

In keeping with the goals of the current research, I do not wish (and will not attempt) to compare these two theories directly. Instead, it is worth noting that while both the cortical re-entrant processing model (Di Lollo et al., 2000; Enns and Di Lollo, 2000) and the dualchannel, sustained-transient view adequately explain the inability of the prime to be processed up to a conscious level, the standard dual-channel sustained transient approach fails to account for the ability of a prime to influence motor responses to the mask (i.e. the phenomenon of masked priming). As outlined in the introduction, and demonstrated through the results obtained in Studies 1 through 4, primes influence motor responses in accordance with their identity (e.g. reaction time to a left arrow mask is faster when the mask is preceded by a left prime arrow compared to a neutral prime). From these results it is evident that the identity of the prime is established on some level, and hence mask activity does not interrupt prime processing at an early, pre-categorical stage. Thus, based on motor performance to the mask stimuli and research revealing the necessity of re-entrant (or feedback) connections from higher to lower visual areas for visual consciousness (see Sillito et a., 1994; Hupe et al., 1998; Lamme and Roelfsema, 2000; Lamme et al., 2002; Ro et al., 2003), I propose that primes are masked from awareness as a result of a mismatch between a descending code and processes occurring in early visual areas (i.e. the cortical re-entrant processing explanation). Furthermore, and more important to the goals of the current research, I assume that the

feedback connections to early visual areas necessary to form a conscious representation are not required in order for a prime to influence action.⁹

6.2.2 Masked priming

The ability of a subliminal stimulus to influence response selection has been repeatedly demonstrated in metacontrast masking reaction time (RT) paradigms (see Taylor and McCloskey, 1990, 1996; Neumann and Klotz, 1994; Dehaene et al., 1998; Ansorge et al., 2002; Schmidt, 2002; Kunde et al., 2003; Vorberg et al., 2003; Breitmeyer et al., 2004). In a typical metacontrast masking RT task, participants are instructed to press a left or right key, with the left or right index finger respectively, according to the identity of a visible target (mask) stimulus. For example, participants may be instructed to press the left key when a left arrow is presented and a right key in response to a right arrow. Unbeknownst to the participants, the target masks are preceded by a subliminal prime stimulus. Responses to the mask (as measured by RT) are faster when the mask is preceded by a congruent prime (i.e. a prime indicating the same response) compared to a neutral stimulus. In contrast, if the mask is preceded by an incongruent prime (i.e. a prime indicating the opposite response), RT to the mask is slower compared to the same neutral stimulus. Thus, metacontrast masking RT paradigms give rise to a perception-action dissociation. Specifically, motor responses are influenced by a prime stimulus that is not consciously perceived.

Having established that motor responses can be influenced by subliminal stimuli, researchers next turned their attention to exploring the mechanism by which this influence arises. In investigating possible mechanisms, researchers have focussed their attention on perceptual and response-related prime processing. For example, researchers have questioned if the influence of a prime on action is governed by (1) associated perceptual processes which enable the identification of the mask to be facilitated under conditions in which the prime and mask are congruent and (2) prime-related activation which may begin to bias response tendencies. Based on results from current research, it appears that prime-related processing influences performance at both perceptual and response-related levels. For example, Bodner and Dypvik (2005) have demonstrated that primes facilitate sensory processing of the

⁹ Feedback connections concerning prime-related activity to early visual areas are absent in the dual-channel, sustained-transient view of metacontrast masking and consequently, unavailable to guide action.

subsequent mask stimulus. In their task, Bodner and Dypvik (2005) instructed participants to categorize target numbers as odd or even (i.e. odd number, press a left key versus even number, press a right key). In addition to finding an overall congruency effect, results indicated an additional benefit in RT (i.e. the fastest RT) on trials in which the prime and mask were identical compared to when the prime and mask indicated the same response was required (i.e. 1-1 versus 1-3) (see also Bodner and Masson, 1997). In accordance with these results, Koechlin and colleagues (1999) found that RT was faster on trials in which the prime and mask were perceptually identical compared to when they were the same on a conceptual level (i.e. 1-1 versus 1-one).

To find support for subliminal visual processing influencing performance at the level of response activation, researchers have turned to masking studies providing electrophysiological indices of motor-related cortical activation during the reaction time interval (see Deheane et al., 1998; Eimer and Schlaghecken, 1998; Leuthold and Kopp, 1998; Jaskowski et al., 2003). In general, this work has demonstrated that the visuomotor processing of a prime within the established stimulus-response set leads to the activation of the corresponding motor response. For example, Leuthold and Kopp (1998) derived the lateralized readiness potential (an index of selective motor preparation), from electrophysiological (EEG) activity recorded during a metacontrast masking experiment in which participants made speeded left or right hand responses to the location of the target stimulus. These authors showed that in addition to obtaining the expected congruency effects in reaction time, the time-course and shape of the readiness potential waveforms were indicative of the masked primes activating the corresponding response at the level of the motor cortex.

While behavioural evidence suggests that prime-related processing influences performance due to both perceptual and response-related activity, current theories put forth to explain the influence of subliminal primes on action have primarily focused on the ability of subliminal stimuli to influence response-related stages. In fact, even before electrophysiological evidence was available, Neumann and colleagues (Neumann, 1990; Neumann and Klotz, 1994), proposed the theory of Direct Parameter Specification (DPS). According to DPS, unconscious visuomotor processing influences performance as a result of a subliminal prime stimulus activating an associated response. Due to the nature of the

stimulus sequence presented in the current research (e.g. in Studies 1 through 4, the primes and masks were both directional arrows and two task relevant stimuli were mapped to two corresponding responses) and the results obtained (e.g. Study 1: the primes took over control of a goal-directed action), I will discuss my results in accordance with theories founded on the assumption that subliminal stimuli influence performance due to response-related activity (i.e. the theory of DPS and the Action Trigger Hypothesis (Kunde et al., 2003; Kiesel et al., 2007)).

The theory of DPS (Neumann, 1990; Neumann and Klotz, 1994) and the Action Trigger Hypothesis (Kunde et al., 2003; Kiesel et al., 2007) adopt a top-down contingency (TDC) framework to explain the ability of subliminal stimuli to influence action. For example, both theories propose that the ability of a subliminal stimulus to influence motor performance is dependent on one's intentions. Specifically, Neumann (1990) and Kunde and colleagues (2003) suggest that participants establish a stimulus-response mapping, based on instructions provided. This mapping (e.g. mapping a left arrow stimulus to a left response and a right arrow stimulus to a right stimulus), creates appropriate release conditions or "action-triggers" for task-defined response alternatives. At the start of each trial, the actiontriggers are activated and waiting for the last visual parameter to uniquely specify the required response (i.e. indicate hand). If an external event matches one of the release conditions, the corresponding response is activated without requiring conscious mediation.

TDC accounts of subliminal processing further suggest that a task relevant prime has an automatic influence on performance. For example, if an incoming stimulus is within the established stimulus-response mapping it will evoke a specific response in an immediate fashion (see Ansorge et al., 2002). In other words, the proposed impact of subliminal information on action can be described as *conditionally automatic* (Bargh, 1992).

While the majority of results obtained from metacontrast masking RT paradigms support current TDC accounts of subliminal visuomotor processing and electrophysiological evidence clearly indicates that a prime is processed up to the level of the motor cortex, the notion of a task relevant prime influencing performance by activating an action trigger is rather vague. Furthermore, current TDC accounts of subliminal visuomotor processing do not indicate how a response actually comes to be initiated. From results obtained in metacontrast masking RT tasks, it does not appear that an overt response is initiated in

accordance with the identity of the prime, even when prime-related processing activates the motor cortex. Thus, it is possible that motor activation by prime-related processing and the influence of a prime on performance may be uncoupled.¹⁰

The relationship between prime-related processing, activation at the level of the motor cortex and response initiation is currently unclear. Perhaps a response is not initiated as a result of prime processing because the corresponding activity in the motor cortex does not achieve a motor activation criterion threshold. If this were the case, a response would only be initiated after additional motor activation had accumulated (which in a prime-mask sequence would involve processes associated with the mask stimulus). In support of the notion of response initiation being mediated by a criterion threshold at the level of the motor cortex, results obtained by Gratton and colleagues (1988) indicate that the occurrence and accuracy of a response can be predicted by examining motor related activity (see also Hanes and Schall, 1996). In the task employed by Gratton and colleagues (1988), participants were instructed to make a response based on the identity of a central letter, displayed within a sequence of 5 letters (e.g. HHHHH, HHSHH). Gratton and colleagues (1988) found that a response was emitted when motor response activation (as measured by the LRP) had achieved a particular fixed level. In other words, the amplitude of the LRP at the time of response onset was constant, regardless of the time at which a response was initiated.

A second plausible explanation regarding the inability of prime-related processing to result in the initiation of a corresponding overt response in metacontrast masking RT paradigms involves the presence of a *decision* module. For example, priming effects triggered by subliminal primes may not be generated directly at the level of the motor cortex but rather exert their influence through a general-purpose decision module which sends a *"signal"* (i.e. neural activation) to the motor cortex regarding the response to be initiated. This proposed explanation for why a response is not initiated as a result of prime processing is very similar to the motor activation threshold mechanism described previously. However,

¹⁰ Minelli and colleagues (2007) have recently demonstrated activation of the motor cortex in the absence of an overt response. In their task, participants were instructed to simply indicate the presence of a visual stimulus. The stimuli were presented above (suprathreshold), at, or below (subthreshold) the psychophysical detection threshold. In addition to finding a LRP for suprathreshold stimuli, Minelli and colleagues also found a reliable LRP for subthreshold stimuli, to which participants did not respond. Thus, activation of the motor cortex does not always lead to an overt physical response, suggesting that activity in the motor cortex and the initiation of a response may be uncoupled (see also De Jong et al., 1990).

in this instance, a response is not emitted until a signal from the decision module is released. Thus, there is an additional visuomotor processing requirement which is not present in the motor activation threshold explanation.

The notion of a decision module dictating response tendencies is consistent with research examining performance to both conscious and unconscious stimuli. For example, Bichot and colleagues (1996) have demonstrated that while neurons in the frontal eye field of monkeys (FEF: a cortical area that responds to visual stimuli and controls purposeful eye movements), can show selectivity for task relevant stimuli at a very early onset (~80 ms) after extensive training, this enhanced processing does not facilitate saccade latencies compared to control conditions.

Furthermore, results obtained by Shlaghecken and colleagues (2003) in a metacontrast masking RT paradigm also reveal that activity in the motor cortex may not be responsible for the influence of a prime on action. Schlaghecken and colleagues (2003), applied 1 Hz repetitive transcranial magnetic stimulation (rTMS) over the left motor or left premotor cortex before requiring participants to complete a metacontrast masking RT task. In previous research, slow frequency rTMS applied over motor cortex has been shown to reduce motor cortex excitability (as reflected by motor evoked potentials) (Chen et al., 1997). In support of this finding, Schlaghecken and colleagues (2003) found that RT was significantly slower after the application of rTMS compared to control conditions. However, and more importantly to the current discussion, priming effects were not influenced by the rTMS. Specifically, RT was still faster on congruent trials compared to incongruent trials and the overall impact of the primes on performance did not change with application of rTMS. This finding, demonstrating that priming effects may be generated at an earlier stage of visuomotor processing.

In accordance with evidence suggesting that a prime's effect may be independent of activity at the level of the motor cortex, Vorberg and colleagues (2003) have put forth an Accumulator Model of Priming (AMP). In general, the AMP is consistent with the tenets of TDC accounts of subliminal processing (i.e. a task relevant prime influences action in a conditionally automatic manner). But, in contrast to TDC accounts, Vorberg and colleagues (2003) assume that a primes' influence on performance is mediated by a general-purpose

decision module. In the AMP, Vorberg and colleagues (2003) model the two response alternatives as "accumulators". The accumulators are established based on instructions provided and each accumulator collects neural evidence for stimuli mapped to its respective response. For example, if a right arrow is mapped to a right response, neural evidence will collect in the right accumulator while a right arrow is residing in a sensory buffer. Vorberg and colleagues (2003) suggest that both primes and masks are equally effective at driving the accumulators and a response is initiated as soon as the accumulated neural evidence for one response versus the other exceeds a critical threshold value.¹¹

The distinction between the AMP proposed by Vorberg and colleagues (2003) and response activation as outlined within TDC accounts of subliminal visuomotor processing is very subtle. Both frameworks suggest that the influence of a prime on performance arises due to response-related activity. In TDC accounts a prime activates a corresponding response by directly releasing an action-trigger, while the AMP proposes that a prime begins to influence responses by providing activity to a decision module. It is tempting to combine the two frameworks and place the proposed "accumulators" at the level of the motor cortex. However, due to the uncertainty of the relationship governing prime-related activity at the level of the motor cortex and the initiation of an overt response, I will keep the decision module as separate from motor cortex when beginning to discuss my results and refer to prime-related response activation as providing input to a corresponding accumulator. In addition, at present, I will assume the primes influence performance in the conditionally automatic manner put forth by current TDC accounts. For example, a prime within the established stimulus-response mapping provides a set amount of neural evidence to its associated accumulator and a response is initiated as soon at the difference in response alternatives (as measured by the difference in neural evidence) reaches a criterion threshold value.

¹¹ Although not stated explicitly by Vorberg and colleagues (2003), I assume that when they refer to response initiation in the AMP model, this indicates that a signal has been sent to the pre-motor and/or motor cortex regarding the action to be completed. The corresponding response is then carried out in accordance with the decision signal arising from the "accumulators".

6.3 Finding 1: Subliminal visuomotor processing can take over the control of a goaldirected movement

To explore the extent to which unconscious visuomotor processes can influence performance I modified typical masked priming procedures, such that the critical prime-mask sequence was displayed during the execution of an already-initiated goal-directed pointing movement (Study 1 and Study 2). Participants were given a fixed movement goal, to complete a rapid movement to a center target location. On the majority of trials, a neutral prime-neutral mask sequence was displayed, cuing participants to continue to point to the center target. On the remaining trials, the neutral mask was replaced with a directional arrow (left or right). The directional mask was the signal for participants to modify their pointing movement so that their finger landed in either the left or the right eccentric target location, according to the direction indicated by the mask. The masks were preceded by neutral or directional arrow primes. In accordance with TDC accounts of subliminal priming I hypothesized that the primes would influence performance in a similar manner to that observed in metacontrast RT tasks (i.e. as demonstrated in the Response Selection task of Study 1 (Section 2.3)). For example, the primes would begin to bias response tendencies, such that earlier modifications would be observed in trajectories in response to the mask when the mask was preceded by a congruent prime compared to a neutral or incongruent prime. Furthermore, the time of trajectory modification would also differ between the neutral and incongruent prime-mask trials, with earlier adjustments in trajectories from the center target observed on trials in which a neutral prime was displayed.

As predicted by TDC accounts, I found differences in the time of trajectory modifications depending on the prime-mask sequence displayed. Participants were much faster to modify their movements in the direction specified by the mask on congruent trials compared to any other prime-mask combination. However, in contrast to TDC predictions, detailed kinematic analysis of the finger in motion revealed that movement trajectories to the center target were modified on-line first in response to the invisible prime and then if necessary, in response to the visible mask. For example on incongruent trials, trajectories were first modified from the center target in the direction specified by the prime. Initial deviations in trajectory were then corrected in response to the mask, approximately 56 ms later (a time corresponding to modifications observed in the neutral prime-directional mask

trials and equal to prime-mask onset asynchrony). These results reveal that visuomotor processing of a subliminal stimulus can take over the control of a visually guided action.

Moreover, the results indicate that the ability of a subliminal stimulus to influence performance depends on task constraints. In other words, response-related activity due to subliminal visuomotor processing does not have the same *automatic* influence on performance between tasks (as proposed by TDC accounts of subliminal visuomotor processing). For example, while the primes may begin to bias response activation in a key press RT task, participants' responses (overt) are almost always consistent with the identity of the mask (typical accuracy greater than 95%, as reported in Studies 1 and 4). In contrast, in a pointing task, the first recorded responses (trajectory deviations) are observed in the direction of the prime, regardless of the relationship of the prime with the subsequent mask. Thus, participants in an RT situation appear to wait until they identify the mask before committing an overt response, while when faced with a pointing task, participants adjust a goal-directed action as a result of prime processing.

6.3.1 Accumulator model of priming

In attempt to explain these findings within an accumulator model of priming (i.e. adapted from Vorberg and colleagues' AMP (2003)), I propose that the criterion threshold necessary to initiate a response is set at a lower level in a pointing task compared to a key press RT task. In fact, the threshold value is set at a low enough level that prime-related activity exceeds the criterion and a response is initiated in accordance with the identity of the prime. The lowering of the criterion threshold in the pointing task consequently eliminates response competition from arising between prime and mask related activity as a prime evoked response is already initiated before the mask begins to exert an influence. After a response is initiated according to the identity of the prime, the corresponding activation returns to baseline levels, allowing the next stimulus (the mask) to be processed without any interference.

The proposal of a fluctuating threshold difference that is dependent on task constraints accurately predicts the results obtained in Study 1 and explains why the primes do not influence performance in the automatic manner proposed by current TDC accounts. However, the claim of a fluctuating threshold difference is based on the pattern of

performance across two very different tasks, in which the sensitivity of the measurements varied greatly. For example, in the RT task, I recorded participants' final overt responses, whereas in the pointing task, I continually monitored the ability of the primes to influence movement (a potentially more sensitive measure of performance). Perhaps if a more continuous measure of performance had been employed in the key press RT task (e.g. electromyography (EMG) or force transducers), results would have indicated that the primes evoked responses at the level of muscle activation and a similar pattern of results to that observed in the pointing task would have been obtained. In other words, results in the key press task would have revealed prime related response activation before the response was completed in accordance with the mask. Thus, based on the results from Study 1, it is unclear if the difference in the impact of subliminal stimuli on performance between the two tasks arises due to modifications in the visuomotor system due to task constraints (i.e. response initiation versus on-line control), or whether the results merely reflect differences in the sensitivity of measurement employed.

The results obtained in Study 3 and Study 4 (Experiment 2) begin to resolve this issue. In these tasks I manipulated the probability of completing a movement in a specific direction. For example, in Study 3, participants were instructed that on the majority of pointing trials in which they were to modify their movement to the center target, they would most often have to complete their point to the left (or right) eccentric target. Similarly in Study 4 (Experiment 2), participants were instructed that on the majority of trials a left arrow would be displayed and they would be required to press the left key. Results in the pointing study revealed that participants modified their trajectories in the direction of the prime only when it pointed in the more probable response direction. In contrast, both directional primes had a similar influence on performance in the key press RT task. Thus, in the pointing task, which potentially employs a more sensitive measure of prime-related activity, we do not observe an influence of the primes on action under certain conditions (e.g. when the prime indicates the less likely response is required), whereas in the RT key press task, employing a less sensitive measure of performance, we observe an influence of all subliminal stimuli on action. The discrepancy between these patterns of results compared to Study 1, indicates that the visuomotor system is indeed modified as a result of task constraints and hence, the results obtained in Study 1 do not reflect differences in the sensitivity of the measurements employed.

In attempt to model the findings of Study 3 and Study 4 (Experiment 2) within an accumulator model of priming, I begin with the assumption that the criterion threshold necessary to initiate a response would have been set at a lower value in the pointing task compared to the RT key press task. I next examine how participants performed on trials in which the neutral prime was displayed under conditions in which a directional mask (and hence a particular response) was biased. In both the pointing and RT tasks, participants were faster to initiate a response in the more probable direction compared to the alternative, less likely response. These results could not have arisen due to differences in subliminal visuomotor processing, as the same neutral prime preceded both directional masks. Instead, these results imply that participants were more willing to commit a response in the more probable direction. In accordance with these findings, similar results have been obtained in choice reaction time studies exploring the relationship of probability events on responses to visible stimuli (see LaBerge et al., 1969; Blackman, 1972; Hawkins et al., 1973; Heurer, 1982). In order to explain these findings, researchers have proposed that a higher-probability response is prepared prior to stimulus onset (Bertelson and Barzeele, 1965; Laming, 1969; Miller, 1988; Gehring et al., 1992).

In keeping with the notion of advanced preparation, I propose that participants selectively adjust the activation level associated with a particular response based on the instructions provided. For example, if a participant is instructed that on the majority of trials a right response will be required, the neural activity associated with the right accumulator is increased before the trial has even begun. This predisposition for the right response, pre-sets the system to favour the more probable response at the time of prime presentation (i.e. the difference in response activation between the accumulators is weighted to favour the more likely response). Because of this initial activation, my accumulator model (with a fluctuating motor activation threshold) predicts that movements will be initiated earlier to the right than the left when the masks are preceded by a neutral prime (or even when presented alone).

Furthermore, this threshold difference between the two accumulators at the time of stimulus onset could potentially impact the influence of left and right primes on responses. For example, in the pointing task there is the possibility that prime-related processing may no

longer be able to achieve the criterion threshold. Specifically, on trials in which the prime points in the less likely response direction, additional activation would be required to counteract participants' intentional bias before a response could be initiated. The neural activity associated with the prime pointing in the less likely response direction would not achieve this threshold level before input from the mask began to activate its associated response, and hence, responses would not be initiated in the direction indicated by the prime. With respect to the RT task, because the threshold for response activation is set at a greater threshold difference, advanced preparation may not change the ability of the primes to influence performance (compared to baseline conditions in which the two directional masks are displayed with equal probability). In this instance prime-related processing traverses the system and begins to activate its associated responses. However, neural activity associated with the mask would still be required in order to achieve the criterion threshold. Thus, the directional primes would have a similar influence on performance, regardless of their relationship with the directional mask (model illustrated in Appendix B).

6.3.2 Visuomotor processes engaged

The predictions of the new accumulator model (in which the motor activation threshold fluctuates depending on task constraints) are consistent with the results obtained in Studies 1, 2 and 3. The demands of the task (response selection versus on-line control) appear to modulate the threshold value required before a response can be initiated. An intentional bias can then increase the baseline level of readiness or activity associated with a particular response, dictating the potential influence of subliminal stimuli on action. However, there is another possible explanation for why the ability of the primes to influence performance differs between our two tasks. This second explanation is closely related to Accumulator Model of Priming put forth in Section 6.3.1, in that I still assume that a specific amount of response activation must be collected in order for a response to be initiated. However, in this second explanation of how primes influence action, I do not assume that input to the "accumulators" arises due to the same visuomotor processes in both tasks (which I imply in the Accumulator Model of Priming, Section 6.3.1). Instead, I propose that the demands of the task change the visuomotor processing stages engaged prior to response initiation. Specifically, task constraints modify the influence of subliminal stimuli on performance by changing the sources of input required by the accumulators in order to initiate a response.

In previous research employing metacontrast masking RT paradigms, it has been suggested that unconscious processing of masked primes could be a signature of the operation of the dorsal visual stream (see Eimer and Schlaghecken, 1998; Jaskowski et al., 2003; Schmidt, 2002). For example, prime processing is mediated by the dorsal stream and influences performance directly by activating a response at the level of the motor cortex. As outlined in Study 2, Section 3.1, I do not believe that exclusive dorsal stream processing can be held accountable for the influence of primes on action observed in all metacontrast masking RT paradigms performed to date. However, results obtained from Study 2 indicate that the processing of a prime for action can be mediated by the dorsal stream under certain task conditions. In Study 2, participants completed the same goal movement performed in Study 1. However, in contrast to Study 1, the movement was completed in a time-frame in which it would have been under dorsal stream guidance. Thus, any adjustments in trajectory observed would have been mediated by the dorsal stream (see Pelisson et al., 1986; Desmurget et al., 1999; Pisella et al., 2000). In Study 2, we still observe deviations in the direction of the prime, indicating that processing within the dorsal stream can be responsible for a prime's influence on action when participants are required to modify a goal-directed movement. These results reveal that neural activation collecting within the motor cortex due to processes occurring in the dorsal visual stream is responsible for the influence of a prime on action (i.e. the sources of input leading to response initiation include processes occurring in the dorsal visual stream and motor cortex).

While processing in the dorsal stream appears to account for the ability of primes to influence performance in a direct manner in the pointing tasks, I propose that distinct processes are engaged during a key press RT. Specifically, I maintain my position that responses in the key press RT task are not mediated exclusively by processes occurring in the dorsal visual stream. Thus, in order for a response to be initiated in a key press task I suggest that responses are governed by processes occurring in the dorsal visual stream, as well as possible processes in the ventral visual stream and/or frontal cortex. In support of this proposal, it has been shown that masked stimuli influence responses in metacontrast masking RT key press tasks under conditions in which the response is defined by semantics (Dehaene

et al., 1998; Kunde et al., 2003) or proper shape recognition (Neumann and Klotz, 1994) – stimulus attributes processed within the ventral stream (Goodale and Milner, 1992; Milner and Goodale, 1995).

Furthermore, while traditional accounts of visual processing suggest that processing within the ventral stream gives rise to conscious awareness (Goodale and Milner, 1992; Milner and Goodale, 1995), it is well documented that areas in the ventral stream can be activated even when stimuli are blocked from awareness (see Marshall and Halligan, 1998; Rees et al., 2000, 2002). For example, Rees and colleagues (2002) recorded activity in category-specific (face) neurons (located within the ventral stream) in a patient suffering from visual extinction. Even in conditions in which the patient failed to perceive the stimulus at a conscious level, Rees and colleagues (2002) still found activation of the category-specific neurons. Finally, it has been shown that corresponding object- or categoryselective neurons in the ventral stream can be activated within 150-170 ms (see Bentin et al., 1996; Thorpe et al., 1996; Liu et al., 2002; Large et al., 2004) and that activity in the frontal cortex can begin to reflect a participant's decision approximately 150 ms after stimulus onset (Van Rullen and Thorpe, 2001). Reaction times observed in metacontrast masking key press RT tasks are typically in the range of 350-450 ms (see Ansorge et al., 2002; Vorberg et al., 2003; Cressman et al., 2006). Given the time of response initiation compared to task relative activity at various levels of the cortex, it would seem that there is time for input from ventral and frontal cortex to influence performance. Thus it is plausible (and I suggest probable) that the influence of the primes on performance in key press RT tasks arises due to visuomotor processes occurring in a distributed cortical network.

6.3.3 Additional considerations

I have put forth two possible mechanisms in order to explain the difference in patterns of results observed between the key press RT tasks compared to the pointing tasks, in which participants were to modify their movements on-line. In the first explanation I assume that the primes are processed in a similar manner up to the level of response activation (i.e. to an "accumulator"). At this point the influence of the primes on performance differs between the two tasks due to a fluctuating activation threshold that is modified depending on task constraints. In the second explanation I suggest that the ability of a prime to influence

performance is governed by visuomotor processing stages engaged prior to response initiation. In the pointing task the primes influence performance directly due to processes occurring in the dorsal stream. In contrast, the key press RT task engages processes within a distributed cortical network (i.e. the dorsal and ventral stream, as well as the frontal cortex).

In both explanations, I have discussed the difference in patterns of results obtained between the two tasks as arising due to the phase of movement in which participants are to complete their responses (i.e. response initiation versus response execution). However, the two tasks differ along other dimensions as well. For example, the number of effectors involved and the ability of participants to modify initial responses differed between the two tasks. In the pointing tasks, participants used only one limb to make a response and the movement was continuous in nature, such that any initial errors could be corrected on-line. In contrast, in the masking RT paradigms employed in the present set of experiments (and those which have been used in typical metacontrast masking key press RT paradigms), participants were required to make a discrete response by pressing a left or right key with the left or right index finger, respectively. Thus, perhaps it is not differences in the phase of movement completed that gives rise to the varying influence of primes on performance, but the number of effectors involved or the nature of the movement itself.

The current research does not allow me to explore the relationship between these variables (i.e. (1) response execution versus response initiation, (2) 1 versus 2 effectors used within the task and (3) continuous versus discrete task) or possible roles they may play in dictating the different visual processes involved in prime processing. However, as outlined in Study 2 (Section 3.4), recent work indicates that perhaps it is not the phase of the movement that determines either the level of the activation threshold or the cortical areas involved in visuomotor processing, but rather the number of effectors involved (see Schmidt, 2002; Adam and Pratt, 2004; Appendix A). For example, Adam and Pratt (2004) have recently demonstrated that in a precue RT task, the number of effectors within the response set determines the pattern of results. Based on their findings, Adam and Pratt (2004) suggest that single-effector (i.e. pointing) and multiple-effector (i.e. key press) tasks are controlled by different mechanisms. Perhaps these different mechanisms reflect changes in an activation threshold or the ability of processing within areas of the cortex to influence behaviour, as I have discussed in Sections 6.3.1 and 6.3.2, respectively.

Or maybe it is the nature of the task that governs how subliminal information is processed for action. In accordance with this proposal, Schall and Bichot (1998) have put forth that the decision rule governing response initiation adapts to the opportunities and demands of the current task. Furthermore, Schall and Bichot (1998) propose that responses following short reaction times tend to reflect the outcome of an averaging decision, whereas responses following longer RT reflect a winner-take-all strategy. To support their claim they draw on results obtained from Groh and colleagues (1997) and Salzman and Newsome (1994), who recorded the nature of eye movements in monkeys under conditions in which area MT (area V5: middle temporal, responsible for detecting motion signals) was electrically stimulated. In the task by Groh and colleagues (1997) monkeys were required to track slowly moving light spots. They found that the pattern of eye movement responses reflected input from both the velocity signal generated by the microstimulation and the velocity signal derived from the visual stimulus (i.e. a vector average decision). In contrast, Salzman and Newsome (1994) found that when monkeys performed an 8-alternative forced choice direction of motion judgement, responses reflected a "winner-take-all" decision process. For example, the monkeys indicated that the direction of motion was either in the direction of the visual stimulus or in direction indicated by the microstimulation.

Although the results discussed in this section do not reveal the mechanism by which subliminal stimuli influence action, it is evident that task demands will influence how a stimulus is processed for action. Research is currently being conducted in order to explore the exact role the following variables - (1) response execution versus response initiation, (2) number of effectors and (3) continuous versus discrete task - play in dictating how a subliminal stimulus is processed for action. At present, I propose that different processes are engaged when a prime is presented within a metacontrast masking key press RT task compared to when it is presented during the execution of a goal-directed movement (either in accordance with an accumulator model (Section 6.3.2) or the visuomotor processing stages engaged (Section 6.3.3)). Furthermore, I suggest that in metacontrast masking key press RT tasks, an additional integration threshold value must be achieved before a response can be initiated.

6.4 Finding 2: The visuomotor system can be modified in response to unconscious events

The results of the pointing studies (discussed in Section 6.3: Finding 1) indicate that subliminal stimuli do not have an automatic influence on performance, as proposed by the top-down contingency framework, and modeled by Vorberg and colleagues' (2003) accumulator model of priming. Instead, the influence of subliminal stimuli on action appears to be dependent on the nature of the task to be completed (e.g. key press RT task or pointing movement). However, these results do not rule out the possibility that within a specific task, top-down contingency accounts of subliminal priming correctly assume that task relevant stimuli evoke a particular response, in an automatic fashion. In order to explore this possibility, I examined the ability of subliminal stimuli to influence performance within a task, when the prime-mask sequence was manipulated.

Specifically, in Study 4 I examined the roles played by conscious intention, unconscious stimulus processing, and more importantly, the potential interaction between the two in a metacontrast masking key press RT task. Similar to the RT tasks discussed in Section 6.2.2, participants completed a choice RT task in which they were instructed to press a left or right key in response to a left or right arrow respectively. Four separate RT tasks were completed in which the stimulus events displayed were manipulated at either a conscious or an unconscious level. Experiment 1 established the impact of subliminal primes on responses to the mask stimuli when the prime-mask sequence was displayed in a typical metacontrast masking RT task. Hence, results obtained in this task were used as a comparison to evaluate possible changes in performance due to experimental manipulations. In Experiment 2, I manipulated participants' expectations (i.e. intentions) regarding the upcoming response by instructing participants that a particular directional mask would appear on the majority of trials. In the third experiment I manipulated an unconscious event by biasing a particular directional prime, such that it was displayed on the majority of trials. Finally, in the fourth experiment, I modified the relationship between conscious and unconscious events by altering the proportion of trials in which the prime and mask were congruent.

From the results obtained in Study 4, it is evident that subliminal stimuli do not evoke a response in accordance with top-down contingency accounts of subliminal priming (Neumann, 1990; Neumann and Klotz, 1994: Kunde et al., 2003; Kiesel et al., 2007), even

within a task. For example, results from Study 4 reveal that although the impact of a specific subliminal stimulus cannot be selectively modulated in a task in which two stimuli are mapped to two response effectors, performance patterns in general (i.e. the visuomotor system) will adjust in response to manipulations of conscious and unconscious events. In particular, I found that visuomotor processing can be modified such that responses to a particular mask are initiated faster than the alternative response when the prime-mask sequence is manipulated at a conscious (Experiment 2) or unconscious level (Experiment 3). In addition, I found that the impact of subliminal stimuli on action can be modulated in response to changes in the relationship between conscious and unconscious events (Experiment 4). For example, when the prime accurately predicts the upcoming response on the majority of trials, it will have a greater influence on performance compared to when it is followed by an incongruent mask on the majority of trials (i.e. indicates the incorrect response). Thus, TDC accounts incorrectly assume that unconscious processes are restricted to activating a corresponding response. Instead, as demonstrated in Study 4, it is evident that the relationship between information provided by the prime and the imperative mask becomes available to the system (on some level) and leads to modulations in subliminal visuomotor processing.

6.4.1 Accumulator model of priming

It is possible that the modifications of the visuomotor system, as demonstrated by participants' performance in Study 4, can be reflected at the "accumulator" level. Thus, I can still model the present results within my version of the accumulator model of priming, while making the following assumptions: (1) in a key press RT task, stimulus-response links are established for the two possible response alternatives, regardless of the probability of completing a particular response, (2) there is no modulation in how a prime is processed up to the level of response activation (i.e. up to level of providing input to an accumulator), and (3) a response is initiated when the difference in neural evidence between the accumulators achieves a constant threshold value for a particular response (e.g. a key press response). I briefly outlined in Section 6.3.1, that the findings obtained in Study 4, Experiment 2 could be explained by participants selectively preparing the more probable response prior to stimulus onset. This advanced preparation pre-sets the system to favour the higher probability

response at the time of prime presentation (i.e. the difference in response activation between the accumulators is weighted to favour the more likely response). Thus, because of this initial activation, the criterion threshold would be achieved earlier on trials in which the more probable response was to be completed, regardless of the prime displayed.

The results obtained in Study 4, Experiment 3, in which a single directional prime was displayed on the majority of trials (biased prime), also indicated that participants were more willing to initiate a particular response. Specifically, participants were faster to initiate the response opposite to the one indicated by the biased prime. To account for this observation, I propose that the system was modified in a similar manner to Experiment 2, such that the activation level of the response opposite to that indicated by the biased prime was higher at the time of stimulus onset. Finally, to explain the results of Experiment 4, within the accumulator model and assumptions put forth, I propose that the gain of the system was modulated depending on the proportion of congruent prime-mask trials displayed. For example, when the prime and mask were congruent on 80% of the trials, the overall gain of the system was increased allowing incoming activity to have a great influence on performance. In contrast, in the experimental block in which only 20% of the prime-mask trials were congruent, the system was *downregulated*, such that prime-related processing could not influence performance to as great an extent as when the prime and mask were congruent 80% of the time.

The predictions of my proposed version of the accumulator model, guided by my assumptions, are consistent with both reaction times obtained and trends in error performance. However, it is also plausible that the visuomotor system may have been modified before the level of response activation or in a different manner at the level of response activation, and the present results still predicted (i.e. assumptions 2 and 3 may be false). For example, the visuomotor system may have been adjusted to facilitate prime-related processing within other areas of the cortex, enabling resulting processes to have a greater impact on the associated response. In support of this notion, Jaskowski and colleagues (2003) have recently demonstrated that in conditions in which a prime and mask are congruent 80% of the time, prime-related activity at the level of the motor cortex (measured by LRP) is enhanced compared to conditions in which the prime and mask are congruent only 20% of the time (see also Barcelo et al., 2000). In addition, it is possible that

the criterion threshold necessary to initiate a response could be modified selectively depending on the probability of a particular response being committed. For example, as a consequence of instruction, the threshold criterion required to initiate a more probable response may be set at a lower level compared to the less likely response alternative. This adjustment within the visuomotor system (at the level of the accumulators), would still predict faster RT in response to the more probable response and allow both directional primes to have a similar influence on performance.

To summarize, the results obtained in Study 4 demonstrate that it is possible to model the two stimulus-response alternatives in metacontrast masking RT key press tasks as accumulators, in which a set difference in activation levels between the two response alternatives is required in order to initiate a response. However, future experiments are required in order to determine the intricacies of the assumptions of the proposed accumulator model and explain how a response comes to be initiated. At present I suggest that the visuomotor system can be modified at the level of response activation (i.e. at the level of the accumulators) and will now outline a possible mechanism for how adjustments in the system arise as a result of unconscious visuomotor processing.

6.4.2 The influence of context on performance

In Experiments 1, 3 and 4 of Study 4, participants were required to press the left and right keys equally often. However, even though participants were given similar instructions across these three tasks, performance patterns in Experiments 3 and 4 differed from the baseline conditions of Experiment 1. In Experiment 3, in which a particular directional prime was presented on 80% of all trials (high probability prime), results indicated that participants began to favour a particular response. Specifically, participants were faster (and more willing) to initiate responses to the mask pointing in the opposite direction to the high probability prime. In Experiment 4 response patterns changed when the proportion of congruent prime-mask trials was manipulated. For example, when the prime and mask were congruent on 80% of all trials, the primes had a greater influence on performance compared to when the prime and mask were congruent on only 20% of all trials.

In attempt to explain how these different results arose across experiments in which the same overt responses were required (e.g. left and right key presses were completed with

equal probability), it is necessary to examine the relationship between the prime and mask (as the only difference between these experiments was the ability of a prime to correctly predict the upcoming response). In Experiment 3, a specific directional prime was displayed on the majority of trials. Thus, because left and right masks were presented with equal probability, the high probability prime was followed by an incongruent mask on a large portion of trials. In contrast, due to the fact that the second directional prime was displayed so infrequently, it was followed by an incongruent mask on a much smaller portion of trials. In Experiment 4, the proportion of trials in which a prime was followed by a congruent mask was manipulated directly and varied between experimental blocks (80%, 50% or 20%). Thus, when participants were completing the 80% congruent block, the two directional primes were followed by congruent masks on the majority of trials.

Within my version of an accumulator model of priming, I have illustrated the system as resolving conflict arising between prime and mask evoked response activation by mask processes compensating for prime-induced activity. Specifically, the mask processes inhibit (overwrite) prime-induced activation, and then begin to activate an associated response. In order to account for the results obtained in Study 4, I propose that inhibitory activity can accumulate in the system at the level of response activation. The accumulation of these inhibitory signals arising due to subliminal conflicts, results in modifications in the visuomotor system, in the absence of top-down intentional guidance. Specifically, as outlined in Section 5.6, I propose that these inhibitory signals accumulate over time as a result of response competition arising between prime and mask related motor activation and modulate the system at the level of response activation (i.e. the accumulators). Hence, the ability of the primes to influence performance is subject to interference due to changes in the system arising without conscious awareness. For example, in Experiment 3, there would be a greater accumulation of inhibitory activity with the response associated with the biased primes. Thus, responses completed in this direction would be completed at a greater latency compared to the alternative response. In Experiment 4, increased levels of inhibitory activity would collect for both left and right responses when the proportion of congruent trials was only 20% compared to 80%, modifying the impact of both directional primes on performance.

In accordance with my suggestion that the visuomotor system is modified due to inhibitory signals accumulating over a sequence of trials, previous experiments have demonstrated that changes in performance can arise due to contextual modulations. For example, Sturmer and colleagues (Sturmer et al., 2002; Sturmer and Leuthold, 2003) have demonstrated that in a typical Simon task (described in Section 1.2.1) in which participants are required to make a response based on the shape of a stimulus, the influence of stimulus location on performance is dependent on the immediately preceding trial (see also Durston et al., 2002). Specifically, the location of the stimulus influences performance only on trials preceded by corresponding trials (i.e. a trial in which the responses evoked by the location of the stimulus and the identity of the stimulus are congruent). If the preceding trial is a noncorresponding trial (i.e. a trial in which the responses evoked by the location of the stimulus and the identity of the stimulus are incongruent), there is no interference arising from location-based coding. To account for these findings, Sturmer and colleagues (Sturmer et al., 2002; Sturmer and Leuthold, 2003), propose that the unconditional (automatic) route which codes stimulus location is subject to modulation and is suppressed after trials in which a conflict has arisen between location- and stimulus-based coding.

It is unclear if the ability of participants to modify their performance as demonstrated by Sturmer and colleagues (Sturmer et al., 2002; Sturmer and Leuthold, 2003), arises due to top-down, intentional suppression of the *"automatic"* location-based channel or reflects changes in the system occurring in the absence of conscious mediation. In a Simon task, the stimuli are visible and available to the conscious system. Thus, it is possible that participants may gain access to stimulus evoked response tendencies and modify the system accordingly in response to consciously perceived conflicts. In line with this proposal, and in contrast to my suggestion that the visuomotor system can be modulated as a result of events arising in the absence of conscious awareness, recent work employing metacontrast masking RT paradigms suggests that intention is necessary in order to modulate the visoumotor system, and hence the impact of subliminal stimuli on performance.

For example, Kunde (2003) has demonstrated that priming effects can only be modulated under conditions in which a conflict between prime and mask evoked responses are consciously perceived on the previous trial. In his task, participants were presented with an arrow prime-mask sequence and instructed to initiate a response based on the direction of the arrow mask. Within the sequence, Kunde (2003) manipulated the visibility of the prime. For example, on some trials participants were aware of the prime and hence, its relationship to the subsequent mask, while on other trials the prime was masked from conscious awareness. Kunde (2003) found that under certain conditions prime-induced response activation could be temporarily suppressed. Specifically, the influence of the prime on performance was suppressed on trials following those in which participants consciously experienced a conflict between the prime and mask induced responses (i.e. incongruent trials in which the prime had been visible). If a conflict arose without awareness (i.e. incongruent trials in which the prime was masked from awareness), the influence of the prime on performance was not modulated on the subsequent trial (see also Appendix C).

Finally, Jaskowski and colleagues (Jaskowski et al., 2003; Wolbers et al., 2006) have also highlighted the role of conscious awareness in modulating the visuomotor system. In a similar experiment to my Experiment 4 (Study 4), Jaskowski and colleagues (2003) manipulated the proportion of congruent prime-mask trials displayed. In accordance with the results of Experiment 4, Jaskowski et al. (2003) found that the primes had a greater impact on performance when the prime and mask were congruent 80% of the time compared to when only 20% of all trials were congruent. However, in contrast to my explanation of the system adapting as a result of the accumulation of inhibitory signals, Jaskowski and colleagues (Jaskoski et al., 2003; Wolbers et al., 2006) proposed that participants strategically made adjustments in the system as a result of monitoring overt error frequency. For example, participants monitored their error performance and modified the system in order to ensure that they reacted as quickly as possible while maintaining a low number of errors. In the instance when the proportion of congruent trials was 80%, these adjustments allowed for information from the prime to be readily carried to motor areas where it activated its corresponding response. In contrast, when only 20% of the trials were congruent, subliminal information was not allowed to influence motor processes to as great an extent.

While the results of Study 4 are in accordance with the results discussed above (i.e. indicate that the influence of subliminal stimuli on performance can be modulated depending on the context of the sequence presented), my explanation is not. In Section 5.5, I have outlined why the adjustments in performance observed in Study 4 are difficult to reconcile with the notion of an intentional modification of the visuomotor system. For example, my

results indicate that changes in performance can arise after a limited number of trials, in which participants commit very few errors. Furthermore, the present results suggest that the system can be modulated in a more specific manner than proposed by Jaskowski and colleagues (2003). Specifically, I have found that that a particular response can be preferentially prepared (activated) as a result of presenting a specific directional prime on the majority of trials. Finally, this is the first study to systematically compare the roles played by conscious intention, unconscious stimulus processing, and more importantly, the potential interaction between the two to an established baseline performance. Thus, based on the present results I propose that adjustments in the visuomotor system, which lead to changes in the ability of subliminal stimuli to influence performance, can occur without conscious awareness (see also Bodner and Masson, 2003).

6.5 Final considerations

6.5.1 Visuomotor signals in rapid chase

Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007) have recently proposed the notion of a rapid chase model to explain the influence of stimuli presented in metacontrast masking RT tasks on performance. According to Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007), prime and mask signals traverse the visuomotor system in a feedforward manner and independently activate a corresponding response. As a demonstration of this phenomenon (i.e. prime and mask signals activating a corresponding response in a sequential manner), Vath and Schmidt (2007) independently manipulated the intensity of the prime and mask colours, as well as prime-mask onset asynchrony in a metacontrast masking task in which participants were required to make a speeded response according to mask colour. Results revealed that the effect of the primes on response activation (as measured by LRP) was independent of the characteristics of the subsequent mask (i.e. intensity of mask colour or time of presentation). Furthermore, responses to the mask were time-locked to the characteristics of the mask, indicating that processes associated with the prime and then the mask independently activated the motor system (i.e. without interference). In accordance with these results, Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007) define two successive stimuli (i.e. the prime and mask) as engaging in a rapid chase if (a) the response is initiated in accordance with the

first prime stimulus, (b) the response is influenced by the mask stimulus before completion, and (c) the response to the first stimulus is initially independent of the second stimulus.

The results from the pointing studies (Studies 1 and 2) demonstrate that the rapid chase criteria put forth by Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007) to explain how primes and masks influence performance can also be reflected at the level of motor output. For example, I found that participants modified their goal directed movements first in the direction of the prime and then, if necessary, corrected initial modifications in response to the visible mask that followed (at a time equivalent to prime-mask onset asynchrony). However, if we look at results from Study 3, in which participants adopted an intentional bias, the motor output does not reflect the prime and mask signals behaving in a rapid chase manner across all trials. Specifically, I found that participants modified their trajectories in the direction of the prime only when it pointed in the more probable response direction. On trials in which the prime indicated the less likely response, one modification in trajectory was observed - in the direction specified by the mask. Do these results indicate that the prime and mask signals were not engaged in a rapid chase under these task conditions?

In attempt to explain the results of Study 3, I proposed that prime-related activity traversed the visuomotor system in a similar manner, regardless of its relationship with participants' intentional bias (discussed in Section 6.3.1). The influence of a particular prime on performance was then dictated by the current state of the system. Thus, this explanation of the present results still assumes that the prime and mask signals were processed in a *rapid chase* manner, fighting sequentially for control of the movement. While I acknowledge that this is only a possible explanation for the results obtained in Study 3, it does raise the possibility that the criteria put forth by Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007), for determining if stimuli are processed in a rapid chase manner, may be too stringent. For example, perhaps the role of intention and the state of the visuomotor system needs to be included on some level in Schmidt and colleagues' (Schmidt et al., 2006; Vath and Schmidt, 2007) rapid chase model.

The pointing results also call into question the assumption that the influence of the prime stimuli on performance arises due a single feedfoward sweep of activation. For example, based on the ability of primes and masks to activate responses in a sequential

manner as outlined in the rapid chase model, and the onset times of prime-related LRP (~200 ms after prime onset), Schmidt and colleagues (Schmidt et al., 2006; Vath and Schmidt, 2007), have proposed that motor activation in response to prime processing is primarily due to the first wave of visual activity that travels through the system in a rapid, feedforward sweep. In its strictest sense, a feedforward sweep refers to the sequential activation of posterior to anterior visual processing areas free of intracortical feedback information (see Lamme and Roelfsema, 2000).

While the majority of the pointing results meet Schmidt and colleagues' (Schmidt et al., 2006; Vath and Schmidt, 2007) rapid chase criteria, based on the present data I cannot determine if the prime-related responses I observed arose due to a single feedforward sweep of activation. Feedback mechanisms in early visual areas can be very rapid (Bullier, 2001; Girard et al., 2001) and there are many feedback and recurrent connections within the visual system (Van Essen et al., 1992). Furthermore, as outlined in Section 6.3.1, activation at the level of the motor cortex can be decoupled from response initiation. Thus, if we examine the latency of prime-related deviations observed (approximately 220 ms), a true measure of the prime's influence on performance, results from the pointing studies suggest that there may have been time for feedback loops to have an influence on preformance. For example, from Lamme and Roelfsema's (2000) meta-analysis of single-cell cortical response studies, the primary motor cortex can be activated within 150 ms of stimulus onset in response to a feedforward sweep of activation. If we add 20-25 ms to this estimate (time required to activate a motor evoked potential (MEP) in the distal upper limb muscles, Ray et al., 2002), we find that 70 ms need to be accounted for. Thus, it is possible that this additional time would allow for visual feedback processing loops to influence performance - which may be a requirement in order for a response to be initiated.

In general, the present data conform to the notion of prime and mask signals traversing the visuomotor system in a rapid chase manner. Furthermore, results from the pointing studies do not discount the possibility that prime-related activity is carried through the visuomotor system and activates a response in a feedforward manner, as I recognize that additional time may be required in order for response activation to accumulate before a response can be initiated. However, this additional time would also allow for possible feedback connections to have an influence on performance. Thus, at present, based on the results obtained in the pointing studies and in accordance with the explanation of how (or why) primes are masked from awareness (Section 6.3.1), I suggest that feedback connections may be required in order to initiate a response. However, these feedback connections would not involve feedback loops to early visual processing areas.

6.5.2 The choice of arrows as stimuli

Jaskowski and colleagues (discussed in Jaskowski and Verleger, 2007) have recently demonstrated that larger priming effects are observed when participants are required to make a response based on the direction of a target arrow compared to situations in which responses are dictated by stimulus shape (i.e. square or diamond). In their priming sequence, three stimuli were presented in rapid succession; a prime, followed by a mask, and then a target to which participants were to make a response. In contrast to the priming effect observed in the present research, this type of stimulus sequence, in which a mask is presented between prime and target onset, gives rise to an inverse priming effect (or negative compatibility effect, see Eimer and Schlaghecken, 1998). For example, RT is shorter and responses more accurate when the prime and target indicate opposite responses are required (incongruent trial) compared to trials in which the prime and target indicate the same response is required (congruent trial). Furthermore, the impact of the prime on performance (i.e. the magnitude of the inverse priming effect) is modulated depending on the stimulus sequence displayed. Specifically, the prime has the greatest influence on performance when the primes and targets are directional arrows and the mask is formed by overlaying the two target arrows (Jaskowski and Przekoracka-Krawczyk, 2005; see also Lleras and Enns, 2004, 2006).

To account for the superior ability of arrow stimuli to influence performance, Verleger et al. (submitted; discussed in Jaskowski and Verleger, 2007) suggest that arrows are "special". In accordance with this proposal, recent evidence in reaction time tasks indicates that the processing of an "endogenous," meaning-based arrow cue leads to the automatic activation of a corresponding response. For example, Hommel et al. (2001) and Kingstone et al. (2003) have shown that visible arrows are capable of producing reflexive shifts of attention when they are presented centrally and known to be spatially nonpredictive. In both studies the reflexive shifts in attention produced reaction time benefits for stimuli presented at the "cued" location.

Thus, a final point of consideration regarding the current results concerns the ability to extend the present findings to indicate how unconscious information is processed for action, in general. In all four studies, I examined the properties of visuomotor processing occurring in the absence of awareness by monitoring participants' responses to a stimulus sequence consisting of directional arrows. Based on these results I have proposed potential mechanisms to explain how subliminal stimuli (in general) are processed for action. However, it is possible that the present results are restricted to situations in which arrow stimuli are displayed. For example, modifications in movement trajectories may not be observed when the response is dictated by a more endogenous stimulus feature (e.g. the colour, shape or semantics of the mask).

The current results do not allow me to address this issue directly. However, it is important to note that the results obtained in the baseline RT task (see Study 4, Experiment 1) are similar to findings obtained when the prime and mask share the same location (Ansorge et al., 2002), shape (Neumann and Klotz, 1994), colour (Schmidt, 2002; Breitmeyer et al., 2004) and semantics (Dehaene et al., 1998; Kunde et al., 2003). Furthermore, Schmidt and colleagues (Schmidt, 2002; Schmidt et al., 2006; Vath and Schmidt, 2007) have recently demonstrated that trajectories can be influenced by colour stimuli presented below the threshold of conscious awareness in a similar manner to that observed in the current research. As well, in a task in which participants were instructed to make a "free" choice to a centrally presented neutral cue by pressing either a left or a right key, Schlaghecken and Eimer (2004), found that subliminally presented prime arrows did not influence free-choice performance. For example, participants completed left and right responses equally often, regardless of the direction of the prime pointing arrow. It was only in blocks of trials in which neutral cue trials were intermixed with right and left target masks, to which participants were required to press the corresponding response key that the directional arrow primes began to bias "free" choices. Thus, given previous results obtained in metacontrast masking paradigms and the fact that all of the stimuli were presented at a central fixation in the present experiments, I am

confident that the present findings can be generalized to indicate how the system responds to processes occurring below the threshold of awareness.¹²

6.6 Conclusion

This research sought to examine the properties of visuomotor processing occurring in the absence of conscious awareness. I found that (1) unconscious visuomotor processing can result in the modification of an overt response, such that a goal-directed movement is adjusted in response to a subliminal stimulus and (2) the visuomotor system can be modified in response to manipulations of the prime-mask sequence presented at an unconscious level. These results imply that subliminal stimuli are not processed in the *conditionally automatic* manner put forth by current top-down contingency accounts of subliminal processing (see Neumann, 1990; Neumann and Klotz; 1994; Kunde et al., 2003; Kiesel et al., 2007). Specifically, subliminal primes within an established stimulus-response mapping do not evoke an immediate and predicted response. Instead, the ability of a prime to influence performance is determined by the state of the system, which is modified depending on task constraints (e.g. stage of movement production and/or the ability of the prime to correctly predict the upcoming response). These adjustments in the visuomotor system can be mediated by intention but also arise due to events occurring in the system at an unconscious level.

In order to explain the ability of subliminal stimuli to influence behaviour I have proposed an accumulator model (adapted from Vorberg et al., 2003), in which adaptations to the state of the system arising due to task constraints are reflected at the level of response activation (i.e. at the accumulators). In this proposed mechanism, sources of input to the accumulators (i.e. neural activation related to a particular response) are similar across tasks. Activity collects in the accumulators until a criterion threshold, measured as the difference in activation levels between the two response alternatives, has been achieved. This criterion threshold can be modulated depending on the task to be completed. However, once the

¹² If the influence of subliminal stimuli, presented during a pointing task, on action is mediated by exclusive dorsal stream processing, some stimuli (e.g. a response defined by semantics), may not lead to direct motor activation.

required criterion threshold has been achieved, a *decision* signal regarding the action to be performed is released.

As a second explanation for how subliminal stimuli influence action I have put forth that pointing tasks and key press RT tasks engage different visuomotor processing areas (i.e. sources of input to the "accumulators" depend on the task to be completed). Specifically, in a pointing task the primes are mediated by processes occurring in the dorsal stream and hence have a direct impact on action. In contrast, a response is not initiated in the key press RT task until processes in a distributed cortical network have been engaged (e.g. the dorsal and ventral visual streams, as well as the frontal cortex). These two explanations are put forth merely as a proposal. The exact mechanism by which subliminal stimuli begin to influence action still remains to be determined. Furthermore, while the present results have demonstrated that unconscious processes can contribute to behaviour to a greater extent than has previously been shown, I by no means suggest that this is the limit to the ability of unconscious processes to influence action. Perhaps future research will indicate that Rothwell (opinion in Prochazka et al., 2000), is correct in suggesting that the only time we are in moment-to-moment control of own actions is in the initial stages of learning a new task (e.g. establishing action-triggers). The rest of the time (99% of our waking life), we do not have voluntary control over our body and movements are performed in the absence of conscious awareness.

6.7 References

- Adam, J.J., & Pratt, J. (2004). Dissociating visual attention and effector selection in spatial precuing tasks. *Journal of Experimental Psychology: Human Perception* and Performance, 30, 1092-1106.
- Ansorge, U., Heumann, M., & Scharlau, I. (2002). Influences of visibility, intentions, and probability in a peripheral cuing task. *Consciousness and Cognition*, 11, 528-545.
- Barcelo, F., Suwazono, S., & Knight, R.T. (2000). Prefrontal modulation of visual processing in humans. *Nature Neuroscience*, 3, 399-403.
- Bargh, J.A. The ecology of automaticity: Toward establishing conditions needed to produce automatic processing effects. *The American Journal of Psychology*, 105, 181-199.
- Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551-565.
- Bertelson, P., & Barzeele, J. (1965). Interaction of time uncertainty and relative signal frequency in determining choice reaction time. *Journal of Experimental Psychology*, 70, 448-451.
- Bichot, N.P., Schall, J.D., & Thompson, K.G. (1996). Visual feature selectivity in frontal eye fields induced by experience in mature macaques. *Nature*, 381, 697-699.
- Blackman, A.R. (1972). Influence of stimulus and response probability on decision and movement latency in a discrete choice reaction task. *Journal of Experimental Psychology*, 92, 128-133.
- Bodner, G.E., & Mason, M.E.J. (1997). Masked repetition priming of words and nonwords:
 Evidence for a nonlexical basis for priming. *Journal of Memory and Langusge*, 37, 268-293.
- Bodner, G.E., & Mason, M.E.J. (2003). Beyond spreading activation: An influence of relatedness proportion on masked semantic priming. *Psychonomic Bulletin and Review*, 10, 645-652.
- Bodner, G.E., & Dypvik, A.T. (2005). Masked priming of number judgments depends on prime validity and task. *Memory and Cognition*, 33, 29-47.
- Breitmeyer, B.G., Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *The Psychological Review*, 83, 1-36.

- Breitmeyer, B.G. (1984). Visual masking: An integrative approach. Oxford, UK: Oxford University Press.
- Breitmeyer, B.G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review and update. *Perception and Psychophysics*, 62, 1572-1595.
- Breitmeyer, B.B., Ro, T., & Singhal, N.S. (2004). Unconscious color priming occurs at stimulus- not percept- dependent levels of processing. *Psychological Science*, 15, 198-202.
- Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, 36, 96-107.
- Chen, R., Classen J., Gerloff, C., Celnik, P., Wassermann, E.M., Hallett, M., & Cohen, L.G. (1997). Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation. *Neurology*, 48, 1398-1403.
- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P.-F., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597-600.
- De Jong, R., Coles, M.G.H., Logan, G.D., & Gratton, G. (1990). In search of the point of no return : The control of response processes. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 164-182.
- Di Lollo, V., Enns, J.T., & Rensink, R.A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, 129, 481-507.
- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E. & Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2, 563-567.
- Driver, J., Mattingley, J.B., Rorden, C., & Davis, G. (1997). Extinction as a paradigm measure of attentional bias and restricted capacity following brain injury. In H.-O. Karnath, & P. Their (Eds.), Parietal lobe contributions to orientation in 3D space (pp. 401-429). Berlin: Springer.

- Durston, S., Thomas, K.M., Worden, M.S., Yang, Y., & Casey, B.J. (2002). The effect of preceding context on inhibition: An event-related fMRI study. *NeuroImage*, 16, 449-453.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation:
 Behavioral and Electrophysiological evidence. Journal of Experimental Psychology:
 Human Perception and Performance, 24, 1737-1747.
- Ellis, R., & Tucker, M. (2000). Micro-affordance: the potentiation of components of action by seen objects. *British Journal of Psychology*, 9, 451-471.
- Enns, J.T., & DiLollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience*, 4, 345-352.
- Gehring, W.J., Gratton, G., Coles, M.G.H., & Donchin, E. (1992). Probability effects on stimulus evaluation and response processes. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 198-216.
- Girard, P., Hupe, J.M., & Bullier, J. (2001). Feedforward and feedback connections between areas V1 and V2 of the monkey have similar rapid conduction velocities. *The Journal of Neurophysiology*, 10, 1563-1573.
- Gratton, G., Coles, M.G.H., Sirevaag, E.J., Eriksen, C.W., & Donchin, E. (1988). Pre- and Poststimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Percetpion and Performance*, 14, 331-344.
- Groh, J.M., Born, R.T., & Newsome, W.T. (1997). How is a sensory map read out? Effects of microstimulation in visual area MT on saccade and smooth pursuit eye movements. *The Journal of Neuroscience*, 17, 4312-4330.
- Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, 15, 20-25.

Hanes, D.P., & Schall, J.D. (1996). Neural control of voluntary movement initiation. *Science*,

274, 427-430.

Hawkins, H.L., MacKay, S., Holley, S., Friedin, B., & Cohen, S. (1973). Locus of the relative frequency effect in choice reaction time. *Journal of Experimental Psychology*, 101, 90-99.

- Heuer, R.H. (1982). Choice between finger movements of different and identical form: The effect of relative signal frequency. *Psychological Research*, 44, 323-342.
- Hommel, B., Pratt, J., Cozato, L., & Godijn, R. (2001). Symbolic control of visual attention. *Psychological Science*, 12, 360-365.
- Hupe, J.M., James, A.C., Payne, B.R., Lomber, S.G., Girard, P., Bullier, J. (1998). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature*, 394, 784-787.
- Jaskowski, P., Skalska, B., & Verleger, R. (2003). How the self controls its "Automatic Pilot" when processing subliminal information. *Journal of Cognitive Neuroscience*, 15, 911-920.
- Jaskowski, P., & Przekoracka-Krawczyk, A. (2005). On the role of mask structure in subliminal priming. *Acta Neurobiologiae Experimentalis*, 65, 409-417.
- Jaskowski, P., & Verleger, R. (2007). What determines the direction of subliminal priming. Advances in Cognitive Psychology, in press.
- Kiesel, A., Kunde, W., & Hoffman, J. (2007). Mechanisms of subliminal response priming. Advances in Cognitive Psychology, in press.
- Kingstone, A., Smilek, D., Ristic, J., Friesen, C.K., & Eastwood, J.D. (2003). Attention, researchers! It is time to take a look at the real world. *Current Directions in Psychological Science*, 12, 176-180.
- Koechlin, E., Naccache, L., Block, E., & Dehaene, S. (1999). Primed Numbers: Exploring the modularity of numerical representations with masked and unmasked semantic priming. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1882-1905.
- Kunde, W., Kiesel., A., & Hoffmann, J. (2003) Conscious control over the content of unconscious cognition. *Cognition*, 10, 198-205.
- Kunde, W. (2003). Sequential modulations of stimulus-response correspondence effects depend on awareness of response conflict. *Psychonomic Bulletin and Review*, 10, 198-205.
- LaBerge, K., Legrand, R., & Hobbie, R.K. (1969). Functional identification of perceptual and response biases in choice reaction time. *Journal of Experimental Psychology*, 79, 295-299.

- Laming, D.R.J. (1969). Subjective probability in choice-reaction time experiments. *Journal* of Mathematical Psychology, 6, 81-120.
- Lamme, V.A.F., & Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23, 571-579.
- Lamme, V.A.F., Zipser, K., & Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive Neuroscience*, 14, 1044-1053.
- Large, M.E., Kiss, I., & McMullen, P.A. (2004). Electrophysiological correlates of object categorization: Back to basics. *Brain Research: Cognitive Brain Research*, 20, 415-426.
- Leuthold, H., & Kopp, B. (1998). Mechanisms of priming by masked stimuli: Inferences from event-related brain potentials. *Psychological Science*, 9, 263-269.
- Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: An MEG study. *Nature Neuroscience*, 5, 910-916.
- Lleras, A., & Enns, J.T. (2004). Negative compatibility or object updating? A cautionary tale of mask-dependent priming. *Journal of Experimental Psychology: General*, 133, 475-493.
- Lleras, A. & Enns, J.T. (2006). How much like a target can a mask be? Geometric spatial, and temporal similarity in priming. A reply to Schlaghecken and Eimer (2006).
 Journal of Experimental Psychology: General, 135, 485-500.
- Marshall, J.C., Halligan, P.W. (1988). Blindsight and insight in visuo-spatial neglect. *Nature*, 336, 766-767.
- Miller, J. (1998). Effects of stimulus-response probability on choice reaction time: Evidence from the lateralized readiness potential. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1521-1534.
- Milner, A.D., & Goodale, M.A. (1995). The visual brain in action. Oxford, UK: Oxford University Press.
- Minelli, A., Marzi, C.A., & Girelli, M. (1997). Lateralized readiness potential elicited by undetected visual stimuli. *Experimental Brain Research*, in press.
- Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research*, 52, 207-215.

- Neumann, O., & Klotz, W. (1994). Motor responses to nonreportable, masked stimuli:
 Where is the limit of direct parameter specification. In C. Umilta and M. Moscovitch (Eds.), Attention and Performance XV: Conscious and nonconscious information processing (pp. 123-150). Cambridge, MA: MIT Press.
- Pélisson, D., Prablanc, C., Goodale, M.A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb II: Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research*, 62, 303-311.
- Pisella, L., Gréa, H., Tilikete, C, Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729-736.
- Prochazka, A., Clarac, F., Loeb., G.E., Rothwell, J.C., Wolpaw, J.R. (2000). What do reflex and voluntary mean? Modern views on an ancient debate. *Experimental Brain Research*, 130, 417-432.
- Ray, J.L., McNamara, B., Priest, A., & Bonifice, S.J. (2002). Measuring TMS stimulus/response characteristics from both hemispheres simultaneously for proximal and distal upper limb muscles. *Journal of Clinical Neurophysiology*, 19, 371-375.
- Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., & Driver, J. (2000). Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain*, 123, 1624-1633.
- Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., & Driver, J. (2002). Neural correlates of conscious and unconscious vision in parietal extinction. *Neurocase*, 8, 387-393.
- Ro, T., Breitmeyer, B., Burton, P., Singhal, N., & Lane, D. (2003). Feedback contributions to visual awareness in human occipital cortex. *Current Biology*, 13, 1038-1041.
- Salzman, C.D., & Newsome, W.T. (1994). Neural mechanisms for forming a perceptual decision. *Science*, 264, 231-237.
- Schall, J.D., & Bichot, N.P. (1998). Neural correlates of visual and motor decision processes. *Current Opinion in Biology*, 8, 211-217.

Schlaghecken, F., & Eimer, M. (2004). Masked prime stimuli can bias "free" choices

between response alternative. Psychonomic Bulletin & Review, 11, 463-468.

- Schlaghecken, F., Munchau, A., Bloem, B.R., Rothwell, J., & Eimer, M. (2003). Slow frequency repetitive transcranial magnetic stimulation affects reaction times, but not priming effects, in a masked prime task. *Clinical Neurophysiolgy*, 114, 1272-1277.
- Schmidt, T. (2002). The finger in flight: Real-time motor control by visually masked color stimuli. *Psychological Science*, 13, 112-118.
- Schmidt, T., Niehaus, S., & Nagel, A. (2006). Primes and targets in rapid chase: Tracing sequential waves of motor activation. *Behavioural Neuroscience*, 120, 1005-1016.
- Sillito, A.M., Jones, H.E., Gerstein, G.L., & West, D.C. (1994). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature*, 369, 479-482.
- Sturmer, B., Leuthold, H., Soetens, E., & Schroter, H. (2002). Control over location-based response activation in the Simon Task: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 1345-1363.
- Sturmer, B., & Leuthold, H. (2003). Control over response priming in visuomotor processing: A lateralized event-related potential study. *Experimental Brain Research*, 153, 35-44.
- Taylor, J.L., & McCloskey, D.I. (1990). Triggering of preprogrammed movements as reactions to masked stimuli. *Journal of Neurophysiology*, 63, 439-445.
- Taylor, J.L., & McCloskey, D.I. (1996). Selection of motor responses on the basis of unperceived stimuli. *Experimental Brain Research*, 110, 62-66.
- Thorpe, S.J., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, 381, 520-522.
- Van Essen, D.C., Anderson, C.H., & Felleman, D.J. (1992). Information processing in the primate visual system: An integrated systems perspective. *Science*, 255, 419-423.
- Van Rullen, R., & Thorpe, S.J. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience*, 13, 454-461.
- Vath, N., & Schmidt, T. (2007). Tracing sequential waves of rapid visuomotor activation in lateralized readiness potentials. *Neuroscience*, 145, 197-208.

Verleger, R., Ewers, T., & Jaskowski, P. (submitted). On the special role of arrow-masked arrows as flankers: Inverse priming depends on types of stimuli and of masks.

- Vorberg, D., Mattleer, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 6275-6280.
- Weisstein, N., Ozoq, G., Szoc, R. (1975). A comparison and elaboration of two models of metacontrast. *The Psychological Reviews*, 82, 325-343.
- Wolbers, T., Schoell, E.D., Verleger, R., Kraft, S., McNamar, A., Jaskowski, P., & Ruchel,
 C. (2006). Changes in connectivity profiles as a mechanism for strategic control over interfering subliminal information. *Cerebral Cortex*, 16, 857-864.

APPENDIX A

A.1 The Task

To determine if prime related activity can take over the control of motor responses in a task that emphasizes response selection, we instructed participants to initiate a response in the direction corresponding to an arrow mask (i.e. left or right). Participants (10 of the 11 participants tested in Study 2) began each trial holding a stylus with their right hand, such that the stylus was positioned in the middle of a home position (circle with a 2 cm diameter, raised approximately 5 mm from a level surface). An infrared-emitting diode was placed at the tip of the stylus and 3D position was monitored using an OPTOTRAK (Northern Digital, Waterloo, Ontario) motion analysis system (spatial resolution 0.01 mm). The tip of the stylus was equipped with a microswitch that provided an analog signal indicating whether or not the stylus was in contact with the surface of the display. The 3D position of the stylus and the status of the microswitch were sampled at 500 Hz. Raw data from the OPTOTRAK were converted into 3D coordinates and digitally filtered using a second order dual-pass Butterworth filter with a low-pass cutoff frequency of 10 Hz.

On each trial a prime-mask sequence was displayed (see Chapter 2 – Response Selection Task or Figure A1). Prime shapes (4 mm x 9 mm) consisted of left-pointing and right-pointing arrows, as well as a neutral shape formed from the superimposition of the two arrows. Masks consisted of larger (23 mm x 28 mm) versions of the same shapes as the primes, with a central cutout. The outer contour of the prime stimuli fit exactly within the inner contour of the central cutout of the masks. In all trials, primes were presented for 14 ms and the prime-mask stimulus-onset asynchrony (SOA) was set at 56 ms. Masks were presented at the same central position as the primes until the pointing response was complete (approximately 250 ms).

In the current task, participants were instructed to react as quickly as possible to the arrow mask by moving the stylus off the home position in the direction corresponding to the mask displayed (e.g. left arrow mask displayed, movement was to be completed to the left of the home position). There was no designated target position per se; however, participants were further instructed that they were to complete the movement as quickly as possible by

making contact with the surface supporting the home position. All prime-mask combinations were displayed with equal probability and participants completed one block of 120 trials.

A.2 Analyses and Results

The start of the movement was designated as the point in time at which the stylus achieved a horizontal velocity greater than 5 mm/s and the end of the movement was determined by the status of the microswitch placed on the tip of the stylus. Movements that were completed in less than 50 ms or completed in the incorrect direction were excluded from analyses (< 4% of all trials).

In order to establish movement responses, we examined path trajectories in the horizontal direction of motion. For each trial, we obtained the maximum point achieved in the trajectory in the horizontal direction opposite to that indicated by the mask. This value was then subtracted from the start position of the corresponding trial. Figure A2 illustrates the average displacement in the incorrect direction before movements were modified in the direction specified by the mask. From these results it is evident that participants had to correct for initial deviations in their trajectories only on trials in which the prime and mask were incongruent and the prime indicated the response opposite to the mask. Thus, based on these findings, it appears that movements were initiated in response to the prime.

To examine the characteristics of prime related responses, we categorized incongruent prime-mask trials according to whether or not they had been initiated in the direction specified by the prime. A trial was considered to have deviated in the incorrect direction (i.e. initiated in the direction of the prime), if the magnitude of the initial deviation was greater than the average deviation achieved in the neutral trials + 2 standard deviations. Based on this criterion we found that 31% of the incongruent prime-mask trials were initiated in the incorrect deviation.

Having classified incongruent prime-mask trials according to their direction of initiation, we next examined reaction time (RT), measured from the time of mask onset, and movement time (MT) across the various prime-mask combinations (i.e. congruent, neutral, incongruent trials initiated in the direction of the prime, and incongruent trials initiated in the direction of the prime, and incongruent trials initiated in the direction of the prime, and Figure A3b mean MT as a function of prime-mask congruency. From these figures it is evident that the incongruent

trials, which began in the direction of the prime, were initiated faster and completed slower than any other prime-mask trials. These observations were consistent with a 2 mask (left or right) by 4 congruency (congruent, neutral, incongruent trials initiated in the direction of the prime, and incongruent trials initiated in the direction of the mask) analysis of variance (ANOVA) completed for both RT and MT. For example, with respect to RT, ANOVA revealed a significant main effect for congruency (F(3,27) = 41.668, p < 0.001) and post hoc analyses (Tukey's HSD, p = 0.05) confirmed that incongruent trials initiated in the direction of the prime had a faster RT than any other prime-mask combination. Congruent trials were also initiated faster than incongruent trials initiated in the direction of the prime, were completed slower than any other prime-mask combination, F(3,27) = 45.809, p< 0.001.

Given that a number of incongruent prime-mask trials were initiated in response to the prime, it is plausible that some of the congruent trials may also have been also initiated as a result of prime related activity. In order to address this issue, we computed a frequency distribution of RT achieved across the different prime-mask congruency combinations (Figure A4). From Figure A4 it is evident that a proportion of congruent prime-mask trials were initiated at a latency corresponding to the incongruent trials in which responses were made to the prime. Thus, we assume that these congruent responses also arose due to prime processing. Furthermore, in Figure A4, we observe a bimodal distribution for RT achieved on incongruent trials. Fast RT on incongruent trials was observed when participants initiated their movements in the direction of the prime, whereas slower RT was observed when participants initiated their responses in the direction of the mask.

Finally Figure A5, displays the frequency distribution of RT achieved for the same participants when they were required to press a left or right key in response to the arrow mask, as opposed to move a stylus. In contrast to Figure A4, RT for incongruent prime-mask trials was not as fast as congruent trials and the majority of responses (> 97% overall) were completed correctly (i.e. in response to the mask).

A.3 Conclusion

A prime can take over the control of a movement, even in a task emphasizing response selection. From the results displayed above, it appears that in order for a response to be initiated in accordance with the prime's identity, the response must be initiated early. Furthermore, there seems to be a greater chance of a prime taking over control of a movement in response selection tasks in which only one limb is involved and the initial movement can be corrected on-line.

A.4 Figures

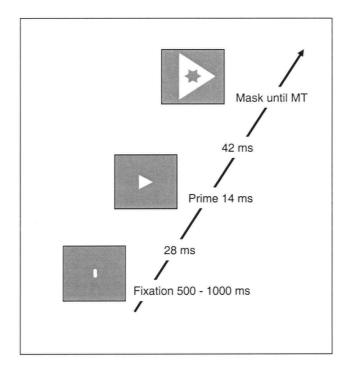


Figure A1. Temporal sequence of a typical experimental trial. Left and right arrows, as well as a neutral stimulus, served as primes. Participants were instructed to make a response based on the direction of the mask arrow (e.g. to move a stylus from a home position in the direction of the mask arrow).

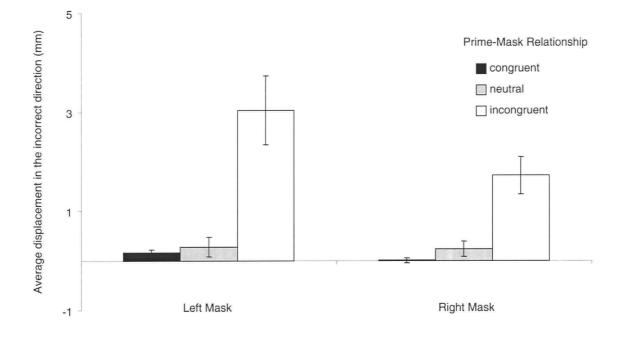
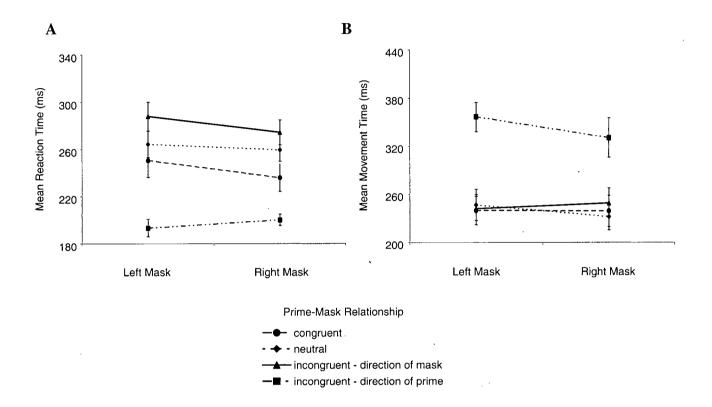


Figure A2. Average displacement in the incorrect direction before movements were modified in the direction specified by the mask. Results are shown for both left and right masks as a function of prime-mask congruency (congruent, neutral or incongruent). Errors bars denote standard error.



<u>Figure A3.</u> (A) Choice reaction times (RT) and (B) mean movement times (MT), to the mask stimuli as a function of prime congruency (congruent (denoted by a circle symbol), neutral (diamond), incongruent trials initiated in the direction of the prime (triangle), and incongruent trials initiated in the direction of the mask (square)). Errors bars denote standard error.

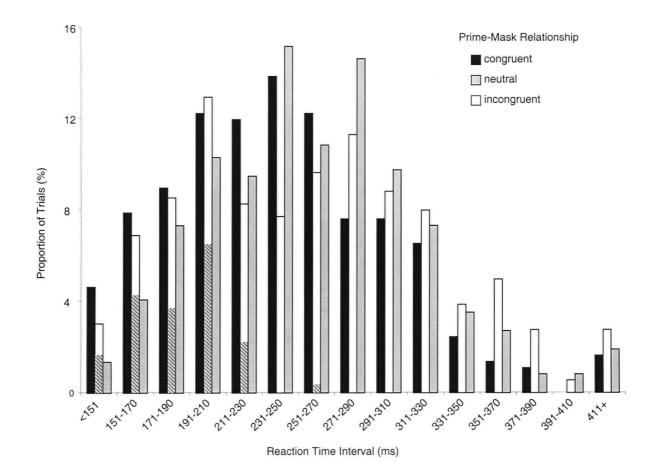


Figure A4. A frequency distribution of RT. Results are displayed as a function of primemask congruency (congruent, neutral or incongruent). In addition, we have indicated the incongruent prime-mask trials on which participants initiated their movements in the direction of the prime (proportion of incongruent trials marked with a diagonal line).

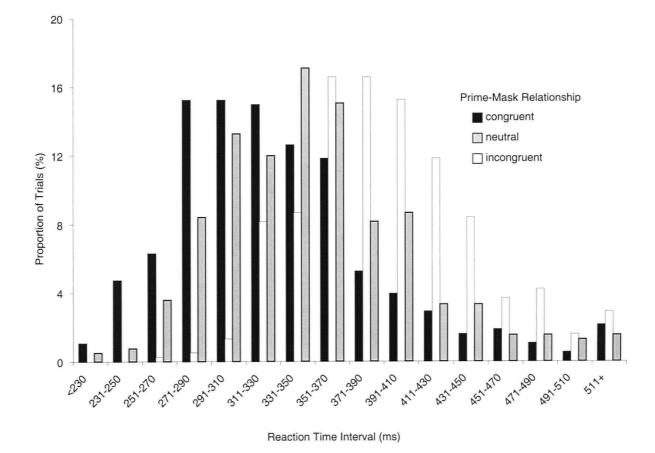


Figure A5. A frequency distribution of RT achieved in a bimanual key press RT task for the same 10 participants. Results are displayed as a function of prime-mask congruency (congruent, neutral or incongruent).

APPENDIX B

B.1 Accumulator model of priming

The following pages illustrate my proposed accumulator model (discussed in Section 6.3.1). This model accurately predicts the results obtained in Studies 1 through 4.¹³

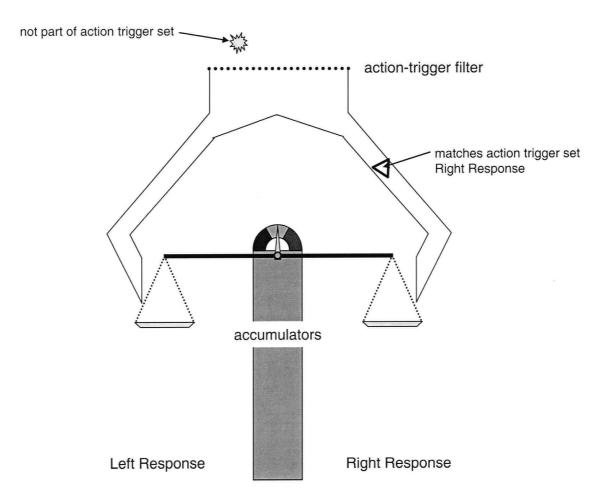
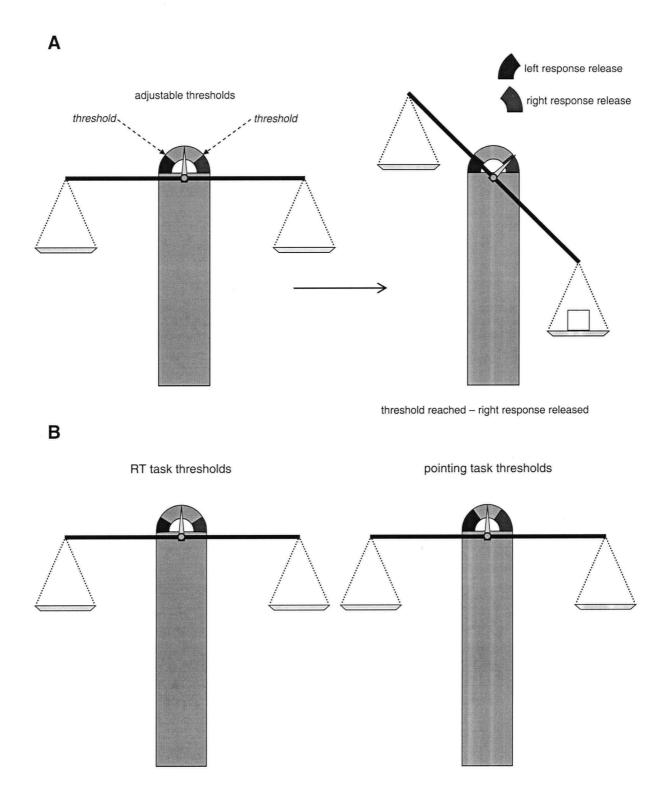


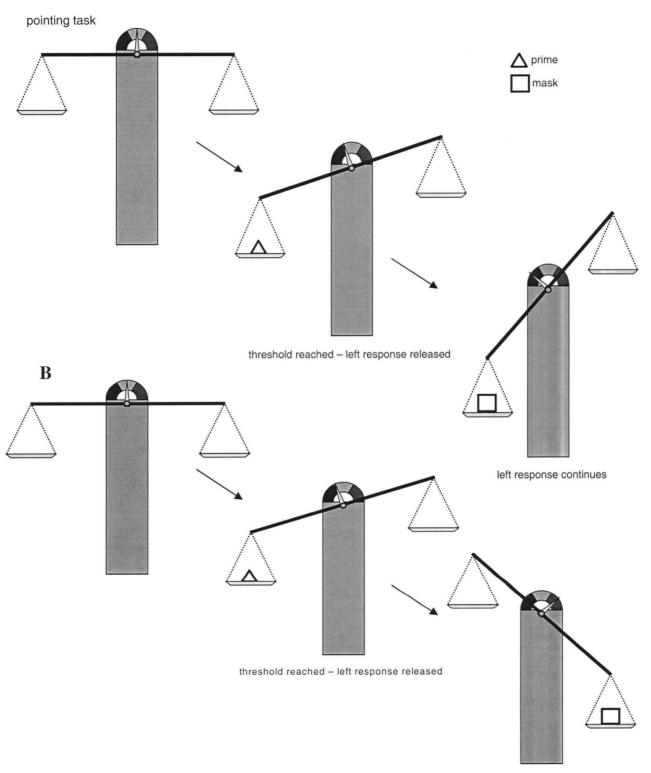
Figure B1. The two response alternatives are modeled as "accumulators," which are established based on instructions provided. Each accumulator collects neural evidence for stimuli mapped to its respective response. For example, if a right arrow is mapped to a right response, neural evidence will collect in the right accumulator while a right arrow is residing in a sensory buffer.

¹³ These figures have been adapted from the originals designed by Dr. Romeo Chua.



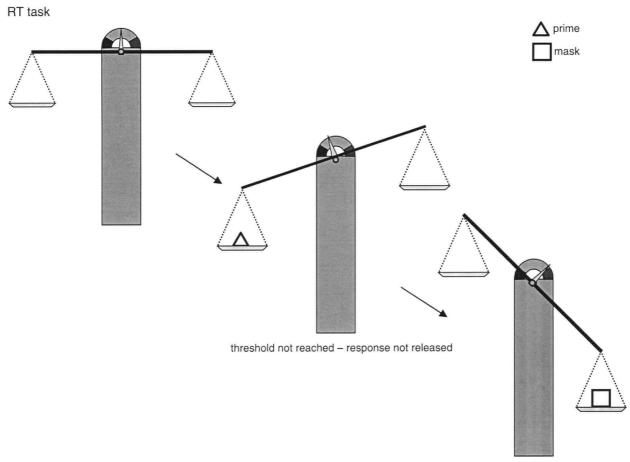
<u>*Figure B2.*</u> (A) A response is released as soon as enough neural evidence has accumulated that a threshold is achieved. (B) The threshold can be adjusted depending on task constraints (e.g. more neural evidence must accumulate before a response is released in a RT task compared to a pointing task).





threshold reached - right response released

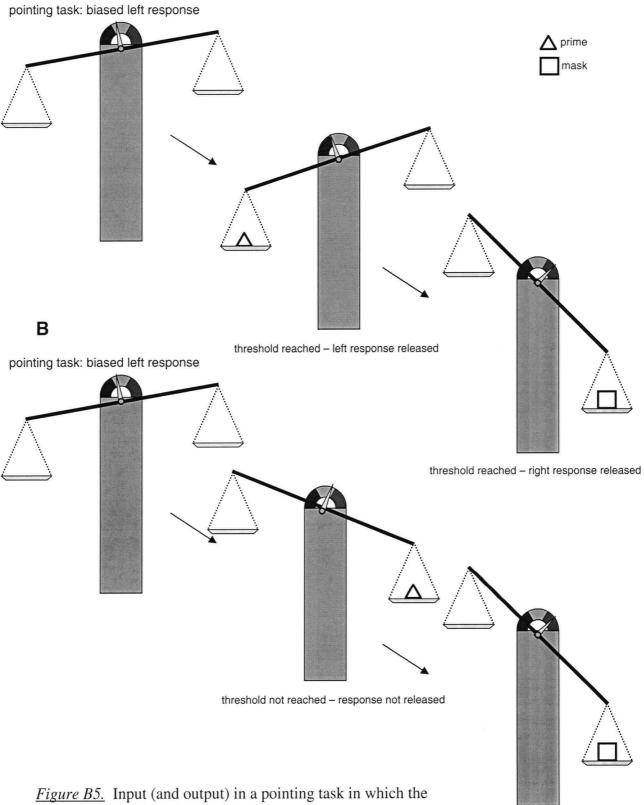




threshold reached - right response released

Figure B4. Input (and output) in a RT task.

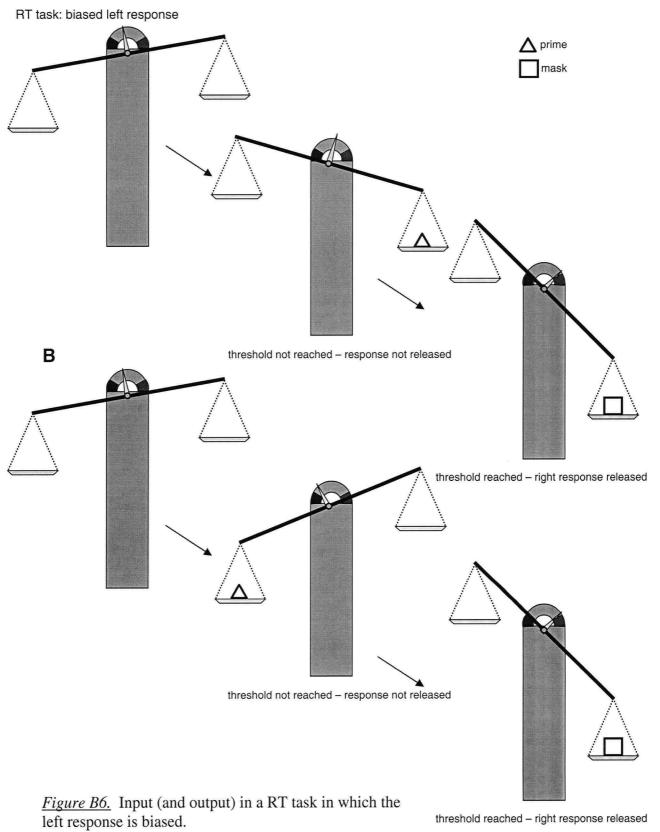
Α



left response is biased.

threshold reached - right response released

Α



threshold reached - right response released

APPENDIX C

C.1 The Task

After completing Experiment 4, Study 4 (Section 5.5), 16 of the 24 participants completed the <u>Mask Response Time</u> task a second time. At this point participants were aware of the presence of the primes and instructed on the ability of the primes to accurately predict the upcoming response. For example, at the start of each experimental block, participants were told of the probability of a congruent prime-mask sequence being displayed. Participants again completed the three experimental blocks; one in which the prime and mask were congruent on 80% of all trials, another when the prime and mask were congruent on 50% of all trials and a third block in which only 20% of the trials were congruent. To complete the session they performed a second <u>Prime Identification</u> task.

C.2 Analyses and Results

Data were analyzed in a similar manner to Experiment 4, Study 4 (Section 5.5). <u>Mask Response Time Task</u>. Mean correct reaction times (RT) for congruent and incongruent trials are displayed as a function of probability distribution in Figure B1a. The difference in RT between incongruent and congruent trials (congruency score) is displayed in Figure B1b. Similar to the results obtained in Experiment 4, Study 4, results indicate a separation in response patterns depending on the proportion of congruent trials displayed. Again, the fastest mean RT was obtained on congruent trials in the experimental block in which the proportion of congruent trials was 80%. These results suggest that the ability of subliminal events to correctly predict the upcoming response influenced the impact of the primes on performance.

Consistent with these observations, a 3 Probability Distribution (80%, 50%, 20%) repeated measures ANOVA revealed a significant main effect, F(2,30) = 5.531, p = 0.01. Post hoc analyses (Tukey's HSD, p = 0.05) indicated that the primes had a greater impact on performance, as demonstrated by a larger congruency score, in the block of trials in which 80% of the trials were congruent ($\bar{x} = 52.7 \text{ ms} \pm 18.9 \text{ SD}$) compared to when only 20% of the trials were congruent ($\bar{x} = 38.0 \text{ ms} \pm 12.3 \text{ SD}$). The differences in congruency scores obtained in the present experiment are very similar to the results obtained in Experiment 4, Study 4 (80% congruent: $\bar{x} = 52.9 \text{ ms} \pm 15.2 \text{ SD}$; 20% congruent: $\bar{x} = 40.7 \text{ ms} \pm 15.8 \text{ SD}$).

Furthermore, performance patterns in terms of errors completed in the present experiment also correspond to participants' performance in Experiment 4, Study 4 (see Table B1). For example, on trials in which participants made an error, a 3 Probability Distribution (80%, 50%, 20% congruent trials) x 2 Mask (left, right) x 3 Prime Congruency (congruent, incongruent with respect to the mask) repeated measures analysis of variance revealed differences depending on the probability distribution and prime congruency (Probability Distribution: F(2,30) = 11.096, p < 0.001, Prime Congruency: F(1,15) = 33.738, p < 0.001, Probability Distribution x Prime Congruency: F(2,30) = 10.683, p = 0.001). Specifically, participants made the most errors on incongruent trials in the experimental block in which the prime and mask were congruent 80% of the time. There was no difference in the number of errors completed on trials in which the prime and mask were congruent, regardless of probability distribution. Furthermore, the number of errors was independent of the mask displayed (Mask: F(1,15) < 1).

<u>Prime Identification Task</u>. Chance performance in this task was 50% (given that directional primes were displayed with equal probability). Mean accuracy collapsed across all primemask sequence combinations was 56.5% \pm 8.1 (SD). This performance did not differ significantly from the chance level of 50% at the p = .05 level ($\chi^2 = 0.250$), or from the performance of these 16 participants in the first <u>Prime Identification</u> task ($\bar{x} = 55.3\% \pm 8.6$ (SD); t(15) < 1).

C.3 Discussion

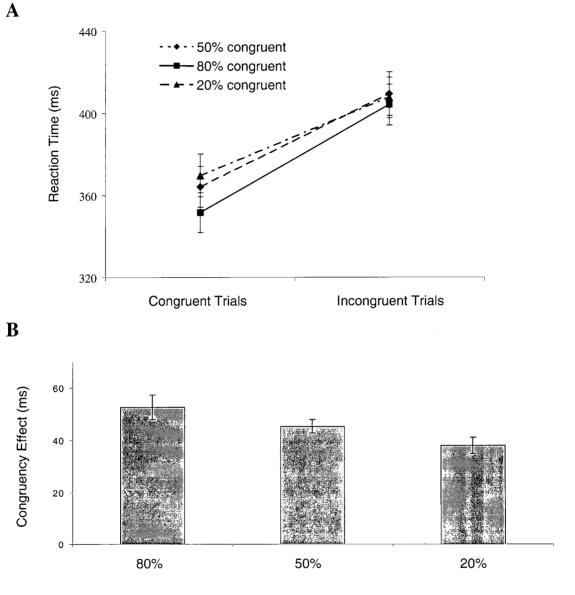
Taken together, the results of the current investigation and Experiment 4, Study 4, suggest that while the impact of a prime on action can be modulated depending on the proportion of congruent prime-mask trials displayed, participants respond in a similar manner regardless of whether or not they are aware of the primes and their relationship with the subsequent mask. Thus, participants cannot strategically (consciously) modify the visuomotor system in order to modulate the impact of unconscious processes on performance

in a RT task. These results are in contrast to results obtained when participants are aware of the primes and the prime-mask sequence is manipulated such that the prime is visible (i.e. the prime acts like a precue; Figure B2). For example, the eight remaining participants from Experiment 4, Study 4, also completed the <u>Mask Response Time</u> task a second time. Like the participants discussed in Appendix B, these participants were aware of the prime and its relationship to the subsequent mask (i.e. the ability of the prime to correctly predict the upcoming response). However, for these participants the prime was displayed for 994 ms and prime-mask onset asynchrony was 1988 ms, making the prime clearly visible. For these participants we observe that the prime's influence on action was eliminated when only 50% of the prime-mask trials were congruent. Furthermore, on the remaining trials participants used the information conveyed by the prime to begin to prepare the most likely response (i.e. the congruent response when the prime and mask were congruent on 20% of all trials and the incongruent response when the prime and mask were congruent on 20% of all trials).

C.4 Table

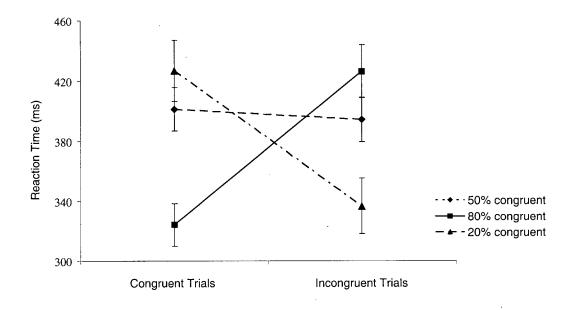
Table C.1. Mean RT (SE) in ms and mean percentage of errors completed (SE) per primemask combination for the present experiment and Experiment 4, Study 4. The first word (i.e. neutral, congruent, incongruent) indicates the relationship of the prime with the subsequent mask. Results are provided for each experimental block (80% = 80% of all trials congruent).

		Congruent – Left Mask	Congruent – Right Mask	Incongruent – Left Mask	Incongruent – Right Mask
Appendix B - Present Experiment	80% - Reaction Time	358 (9)	345 (11)	416 (11)	392 (12)
	80% - Errors	2.1 (0.7)	1.9 (0.5)	11.3 (2.6)	9.7 (1.8)
	50% - Reaction Time	371 (10)	358 (11)	416 (11)	403 (11)
	50% - Errors	1.0 (0.4)	0.8 (0.4)	5.4 (1.3)	4.3 (1.2)
	20% - Reaction Time	379 (11)	361 (10)	417 (10)	398 (10)
	20% - Errors	2.7 (1.4)	1.5 (0.9)	5.0 (01.1)	4.4 (1.1)
Experiment 4, Study 4	80% - Reaction Time	360 (9)	353 (9)	405 (9)	415 (9)
	80% - Errors	1.3 (0.4)	0.4 (0.2)	9.1 (1.7)	6.0 (1.4)
	50% - Reaction Time	366 (10)	353 (8)	400 (8)	412 (9)
	50% - Errors	0.6 (0.3)	0.7 (0.3)	5.6 (1.0)	3.1 (0.8)
	20% - Reaction Time	367 (9)	358 (9)	397 (8)	409 (8)
	20% - Errors	0.8 (0.4)	1.0 (0.6)	2.9 (0.9)	3.0 (0.8)



Proportion of Congruent Trials

Figure C1. (A) Choice reaction times (RT) on congruent and incongruent trials as a function of the proportion of congruent prime-mask trials displayed (80% (denoted by a square symbol), 50% (diamond), 20% (triangle)). (B) The overall priming effect (congruency score) obtained for each of the three experimental blocks in which the proportion of congruent prime-mask trials was varied (80%, 50%, or 20% congruent). The congruency score was calculated as the difference in mean RT between incongruent and congruent prime-mask trials. Error bars denote standard errors.



<u>Figure C2.</u> Choice reaction times (RT) on congruent and incongruent trials as a function of the proportion of congruent prime-mask trials displayed (80% (denoted by a square symbol), 50% (diamond), 20% (triangle)). The prime-mask sequence was manipulated such that the prime was clearly visible. Errors bars denote standard error.

APPENDIX D

UBC Research Ethics Board Certificate of Approval



The University of British Columbia Office of Research Services **Behavioural Research Ethics Board** Suite 102, 6190 Agronomy Road, Vancouver, B.C. V6T 1Z3

CERTIFICATE OF APPROVAL -AMENDMENT & RENEWAL

PRINCIPAL INVESTIGATOR:	DEPARTMENT:		UBC BREB NUMBER:
Romeo Chua	UBC/Education/Hu	man Kinetics	H03-80057
INSTITUTION(S) WHERE RESEAR	CH WILL BE CARR	IED OUT:	
Institution			Site
UBC Other locations where the research will be co N/A	onducted:	Point Grey Site	
CO-INVESTIGATOR(S): Erin Cressman Melanie L Lam Brendan Cameron Ian M. Franks			
James T. Enns			
SPONSORING AGENCIES:			
Natural Science Engineering Resear	ch Council		
PROJECT TITLE:			
Sensory and Perceptual Contribution	is to the Preparation	and Execution of	f Goal-Directed Action

CERTIFICATE EXPIRY DATE: March 27, 2008

	AMENDMENT TE:
Version	Date
1.1	March 5, 2007
	APPROVAL DA March 27, 2007 Version

The application for continuing ethical review and the amendment(s) for the above-named project have been reviewed and the procedures were found to be acceptable on ethical grounds for research involving human subjects.

Approval is issued on behalf of the Behavioural Research Ethics Board and signed electronically by one of the following:

Dr. Peter Suedfeld, Chair Dr. Jim Rupert, Associate Chair Dr. Arminee Kazanjian, Associate Chair Dr. M. Judith Lynam, Associate Chair Dr. Laurie Ford, Associate Chair