

Mechanisms of Intentional Binding and Sensory Attenuation: The Role of Temporal Prediction, Temporal Control, Identity Prediction, and Motor Prediction

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Sensory processing of action effects has been shown to differ from that of externally triggered stimuli, with respect both to the perceived timing of their occurrence (intentional binding) and to their intensity (sensory attenuation). These phenomena are normally attributed to forward action models, such that when action prediction is consistent with changes in our environment, our experience of these effects is altered. Although much progress has been made in recent years in understanding sensory attenuation and intentional binding, a number of important questions regarding the precise nature of the predictive mechanisms involved remain unanswered. Moreover, these mechanisms are often not discussed in empirical papers, and a comprehensive review of these issues is yet to appear. This review attempts to fill this void. We systematically investigated the role of temporal prediction, temporal control, identity prediction, and motor prediction in previous published reports of sensory attenuation and intentional binding. By isolating the individual processes that have previously been contrasted and incorporating these experiments with research in the related fields of temporal attention and stimulus expectation, we assessed the degree to which existing data provide evidence for the role of forward action models in these phenomena. We further propose a number of avenues for future research, which may help to better determine the role of motor prediction in processing of voluntary action effects, as well as to improve understanding of how these phenomena might fit within a general predictive processing framework. Furthermore, our analysis has important implications for understanding disorders of agency in schizophrenia.

Keywords: intentional binding, sensory attenuation, temporal attention, predictive coding, forward action models

The phenomena of sensory attenuation and intentional binding are widely investigated in the domain of voluntary action control. Sensory attenuation refers to the observation that external events that are triggered by human actions are attenuated,

in terms both of their phenomenology and of their cortical response (e.g., Blakemore, Wolpert, & Frith, 1998; Schafer & Marcus, 1973). Intentional binding refers to the finding that an action and an ensuing sensory effect are perceptually attracted toward one another in time (bound), as compared to when either event occurs in isolation (e.g., Haggard, Clark, & Kalogeras, 2002). Both of these phenomena are normally thought to result from forward action models, such that when an action effect is predicted it results in an altered phenomenal experience of the sensory event (Blakemore, Wolpert, & Frith, 2000; Haggard et al., 2002). In this review we systematically assess whether previous experiments support the assertion that sensory attenuation and intentional binding are generated by action prediction mechanisms and not other processes such as temporal prediction, temporal control, or a general form of identity prediction. In addition, we discuss the role of causality and agency belief in these phenomena and the implications of our framework for understanding disorders of agency in schizophrenia.

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That predictive action mechanisms can alter one's experience dramatically is indisputable. For instance, although the image on the retina changes as you move your eyes, you experience a stable visual world (contrary to when your eyes are moved by gently pushing on the corner of your eye). Sensory attenuation and intentional binding are often reported to be extensions of this finding and explained by similar forward action models. Among the first to do so were Blakemore and colleagues (Blakemore, Frith, & Wolpert, 1999; Blakemore et al., 1998, 2000). Blakemore et al. (1998) investigated the phenomenon that it is impossible to tickle oneself (e.g., Weiskrantz, Elliott, & Darlington, 1971). Participants controlled a robotic arm with one hand that was used to tickle their other hand. Activity in somatosensory cortex was reduced when the robot was controlled by the participants rather than by the experimenter. In another experiment, Blakemore, Frith, and Wolpert (1999) found that introducing a spatial or temporal perturbation to participants' self-stimulation led to an increase in the perceived ticklishness. The model shown in Figure 1, adapted from Wolpert, Ghahramani, and Jordan (1995), suggests that at the same time that the motor command is sent, an efference copy that enables the system to predict the sensory consequences of one's action is produced. This predicted effect is compared to the actual observed sensory event, and a sensory discrepancy is calculated. When the two signals match, the system is able to "cancel out" the effect of sensation caused by one's action. Haggard et al. (2002) suggested that precisely the same forward model may be the cause of the intentional binding effect. As such, both these phenomena are commonly described to be the result of a match between the predicted and observed effects of one's action. Indeed, Waszak, Cardoso-Leite, and Hughes (2012) recently proposed a preactivation account, which provides a plausible common mechanism for sensory attenuation and intentional binding based on action-effect prediction.

These forward models are often described as being important for motor control (Wolpert et al., 1995), so they must necessarily be

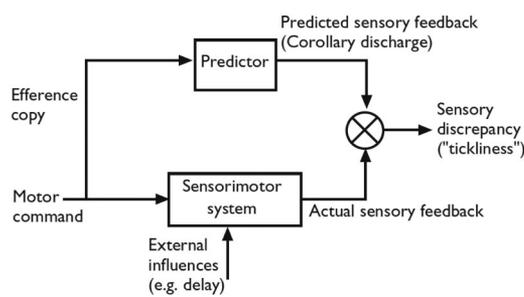


Figure 1. A model from Blakemore et al. (2000) for determining the sensory consequences of one's action. When one performs an action, an efference copy is generated; this allows a forward model to predict the effects of the action (the corollary discharge). These predicted consequences are compared with the observed action effect. When a mismatch is introduced by external influences (e.g., a delay or spatial perturbation in the somatosensory effect of one's action), a discrepancy is detected by the comparator. When there is a match between the expected and observed effect, the predicted effect is "canceled" from the experience, resulting in sensory attenuation. From "Why Can't You Tickle Yourself?" by S.-J. Blakemore, D. Wolpert, and C. Frith, 2000, *NeuroReport*, 11, p. R12. Copyright 2000 by Wolters Kluwer Health. Reprinted with permission.

very specific with regard to the action being performed. If sensory attenuation and intentional binding result from such action prediction mechanisms, they should be "prediction specific." That is, they should be apparent when the stimulus is consistent with a specific effect prediction compared to when it is not. However, as described below, the vast majority of experiments on both sensory attenuation and intentional binding do not compare predicted and unpredicted action effects but instead compare self-triggered with externally triggered stimuli. As we discuss in detail below, such contrasts differ in a number of processes other than motor prediction.

Predictive Mechanisms in Action Selection

Note that we do not question the existence of effect-specific forward action models. Research in ideomotor action does provide strong evidence of effect-specific prediction. The ideomotor theory proposes that voluntary actions are selected on the basis of their learned environmental consequences (e.g., Harless, 1861; James, 1890; Lotze, 1852; for a recent review, see Shin, Proctor, & Capaldi, 2010), such that individuals predict or internally activate the perceptual consequences of their actions (e.g., Elsner and Hommel, 2001; Greenwald, 1970; Herwig, Prinz, & Waszak, 2007; Prinz, 1997). By extension, performing an action involves the same representation as perceiving the associated effect. The ideomotor principle has been shown to be effect specific, such that different action effects are associated with specific actions. For example, Elsner and Hommel (2001) trained participants to associate left- and right-hand keypresses with high and low frequency tones. In a subsequent test phase participants were required to respond to the tones that had previously been presented as action effects. Those participants who received a congruent mapping (i.e., the stimulus-response mapping was the same as the previously learned action-effect mapping) were significantly faster and more accurate. Moreover, the learned associations were found to influence participants' free choices regarding which button to press. These results highlight that motor behavior can be influenced by a stimulus that has previously been associated with a particular action and that can interfere with a new instruction to make appropriate stimulus guided actions. Similarly, learned action-effect contingencies have been found to produce interference dependent on the predicted sensory effect. Kunde (2001) showed that participants were slower in responding to a central target with either a left- or a right-hand button press, if the effect of their action was spatially incongruent with the button press. These effects and more recent replications and extensions (Kunde, 2003; Pfister, Kiesel, & Melcher, 2010; see also Waszak & Herwig, 2007) show that selection or execution of an action entails the internal anticipation of the specific sensory effect the system expects the given action to bring about in the environment. Recent neuroimaging evidence further supports the assumption that action preparation includes the representation of expected action effects (Kühn, Seurinck, Fias, & Waszak, 2010). The current review is not meant to appraise whether action effect prediction exists. Rather, our aim is to determine the extent to which existing evidence of sensory attenuation and intentional binding supports the assumption that these phenomena are genuinely caused by motor prediction mechanisms. As we discuss below, researchers interested in this latter issue may profit from employing techniques similar to

those described above. However, first we briefly describe the methodologies typically employed in investigating sensory attenuation and intentional binding and assess the processes that differed between the experimental and control conditions used in these experiments.

Sensory attenuation has been reported as a perceptual phenomenon by researchers using subjective report (Blakemore, Frith, & Wolpert, 1999), signal detection theory methodology (Cardoso-Leite, Mamassian, Schütz-Bosbach, & Waszak, 2010), and subjective equality judgments (e.g., Sato, 2008), as well as a neurophysiological phenomenon measured with event-related potentials (ERP; e.g., Aliu, Houde, & Nagarajan, 2009; Baess, Jacobsen, & Schröger, 2008; Martikainen, Kaneko, & Hari, 2005) and neuroimaging methods (Blakemore et al., 1998; Blakemore, Wolpert, & Frith, 1999). Intentional binding is often measured by asking participants to retrospectively report the time of an action or an action effect by reporting the position of a moving clock hand (e.g., Haggard et al., 2002, described in detail below; clock method adapted from Libet, Gleason, Wright, & Pearl, 1983). Other methods include motor synchrony tasks (e.g., Cravo, Claessens, & Baldo, 2011), time estimation (e.g., Engbert, Wohlshlager, Thomas, & Haggard, 2007), or replication tasks (e.g., Humphreys & Buehner, 2009, 2010). Recent research (e.g., Moore, Ruge, Wenke, Rothwell, & Haggard, 2010) suggests that the shift of the perceived time of the action and the action effect are caused by postdictive and predictive processes respectively (although see Moore & Haggard, 2008, who suggest that the shifted perceived action time may be a combination of pre- and postdictive processes). Because our aim in this review is to assess predictive mechanisms on the processing of sensory action effects, we discuss only the data regarding the shift in the perceived time of the action effect. Experiments that measure binding using time estimation or replication will be excluded, as they cannot differentiate the contributions of shifts in perceived time of the action from shifts in the perceived time of the effects. This review focuses on the exact nature of the predictive mechanisms that have been observed to influence action-effect processing in previous studies and relates these studies to findings in other research areas, such as temporal attention, repetition suppression, and sensory prediction. We also discuss the types of contrasts that might be fruitful in further understanding the processes involved in attentional binding and sensory attenuation.

In particular we focus on temporal prediction, temporal control, non-motor identity prediction, and motor identity prediction. In the subsequent sections we discuss which of these processes differed in previous published accounts of attenuation and binding. The processes that form the basis of this review are defined below:

- Temporal prediction is defined as the ability to predict the point in time at which a sensory event will occur.
- Temporal control refers to using one’s action to control the point in time at which a stimulus will occur. As stimulation here is controlled by the action, temporal control will in most cases include precise temporal prediction.
- Non-motor identity prediction refers to being able to predict the precise stimulus that will appear. In this instance the prediction of the identity of the stimulus is not dependent on any actions performed by the participant.
- Motor identity prediction refers to prediction of the identity of a sensory event based on an action performed by the participant.

Before assessing how previous experiments fit this framework we describe the possible ways in which these different processes might be manipulated. Table 1 and Table 2 show a number of hypothetical conditions that, when contrasted, differ in terms of the four processes. The conditions in Table 1 (condition types 1 to 3) all include only one possible stimulus (or action effect for condition type 3), and the action condition (condition type 3) includes only one possible action. These conditions are listed in ascending order in terms of the number of processes involved. In condition type 1, stimuli are externally triggered at an unpredictable time (see Figure 2A). This condition involves only non-motor identity prediction (because only one stimulus is presented, its identity is always known) and none of the other processes (because the stimulus is not a result of the participant’s action and is not predictable in time). This type of condition is often used in experiments as a control condition to simulate an unexpected event. Condition type 2 (a and b) differs from type 1 only in that the externally generated stimulus appears at a fixed time after trial onset or after a cue (or a transcranial magnetic stimulation pulse).

Table 1
List of Representative Conditions and Contrasts Typically Used for Investigating Sensory Attenuation and Intentional Binding

Condition type or contrast	Condition or contrast description	Temporal prediction	Temporal control	Non-motor identity prediction	Motor identity prediction
1	Externally triggered stimulus at unpredictable time			✓	
2a	Externally triggered stimulus at a predictable time after trial onset	✓		✓	
2b	Externally triggered stimulus cued by a warning stimulus (or a TMS pulse)	✓		✓	
3	Action-triggered stimulus	✓	✓	✓	✓
Contrast 3-1	Condition type 3 minus condition type 1	X	X		X
Contrast 3-2	Condition type 3 minus condition type 2		X		X

Note. Each condition includes a tick mark under the processes involved. Each contrast includes an X under the processes that differ between the conditions being contrasted. TMS = transcranial magnetic stimulation.

Table 2
List of Hypothetical Conditions and Contrasts That Might Be Usefully Employed to Isolate the Processes Involved in Sensory Attenuation and Intentional Binding

Condition type or contrast	Condition or contrast description	Temporal prediction	Temporal control	Non-motor identity prediction	Motor identity prediction
A	Externally triggered stimulus at an unpredictable time whose identity is unknown				
B	Externally triggered stimulus at a predictable time whose identity is unknown	✓			
C	Action triggers one of two (or more) different stimuli whose identity is unknown	✓	✓		
D	Cue predicting the identity and timing of the stimulus	✓		✓	
E	Action triggers one of two different stimuli whose identity is predicted by a sensory cue	✓	✓	✓	
F	One action triggers one stimulus; an alternative action predicts a different stimulus	✓	✓	✓	✓
Contrast B-A	Condition type B minus condition type A	X			
Contrast C-B	Condition type C minus condition type B		X		
Contrast E-D	Condition type E minus condition type D		X		
Contrast E-C	Condition type E minus condition type C			X	
Contrast F-E	Condition type F minus condition type D				X

Note. Each condition includes a tick mark under the processes involved. Each contrast includes an X under the processes that differ between the conditions being contrasted.

In each of these situations, participants would be able to anticipate the point in time at which a stimulus appears, and in that sense they would have temporal prediction of the stimulus onset (over and above the non-motor identity prediction). Condition type 3, presented in Figure 2B, includes an action to trigger the stimulus. In this condition type, participants make self-paced voluntary actions that trigger the stimulus. In this instance participants not only can predict the timing and identity of the stimulus but can also directly control its onset and identity, thus providing temporal control and motor identity prediction.

The vast majority of studies on sensory attenuation and intentional binding contrast condition type 3 with condition type 2 or 1 (as shown in Figure 2), as this compares action-triggered and externally triggered events. However, Table 1 reveals that the contrast 3-1 covers three of the four processes, namely, temporal prediction, temporal control, and motor identity prediction. Similarly, the contrast 3-2 covers both temporal control and motor identity prediction. It is, thus, not possible to isolate the role of each of these processes on an observed difference between the conditions.

The conditions shown in Table 2 (types A to F) include stimuli of a number of different identities that either are externally triggered or result from one of two (or more) actions. The conditions are ordered in terms of the number or complexity of processes involved, with a selection of these conditions illustrated in Figure 3. Condition type A (see Figure 3A) consists of an externally triggered stimulus of an unpredictable identity at an unpredictable time and includes none of the four processes. Condition B differs only in that the timing of the externally generated stimulus is known, thus providing temporal prediction. In condition type C (see Figure 3B) the participant’s voluntary action triggers a stimulus with an unpredictable identity. This condition includes temporal prediction and temporal control but no identity prediction. Condition type D involves a cue to inform participants of both the identity and the timing of the stimulus. In this condition, participants have temporal prediction and non-motor identity prediction but no temporal control or motor identity prediction because no action is performed. Conditions E and F both include voluntary actions that trigger the action effect. However, in Condition E the identity of the effect is not determined by the action but rather by

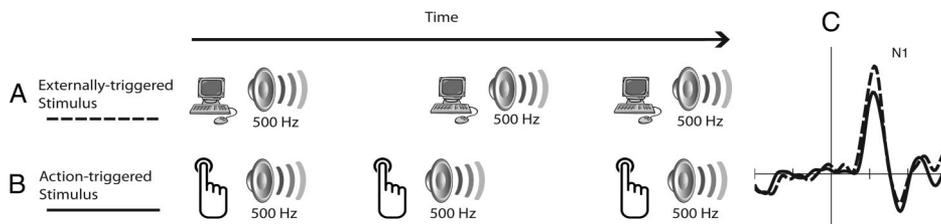


Figure 2. An example of conditions typically used to study sensory attenuation. In the first condition (2A), 500-Hz tones are presented at randomly selected time intervals triggered by the experimental computer. For action-triggered stimuli (2B), participants perform self-paced voluntary actions with their right index finger; these actions trigger the onset of a 500-Hz tone. The comparison between two such conditions is typically associated with attenuation of the primary auditory N1 response around 100 ms after the onset of the tone (2C).

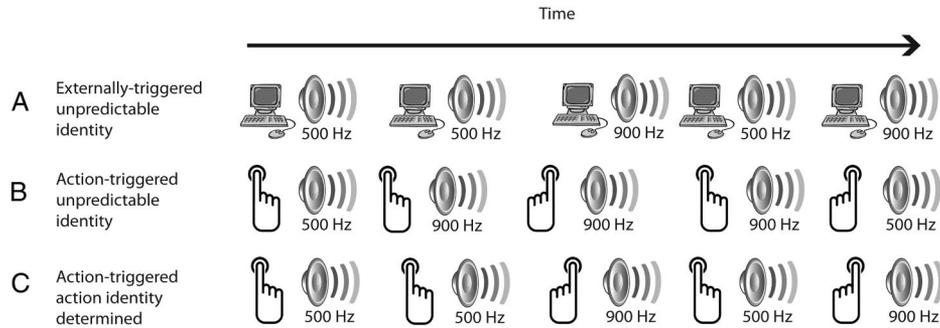


Figure 3. A subset of stimuli presented in Table 2. A: One of two tones (500 Hz or 900 Hz) is presented at random time intervals selected by the experimental computer. B: Participants perform left- and right-hand voluntary actions at self-paced intervals. Their action triggers the onset of the stimulus, but its identity (500 Hz or 900 Hz) is randomly determined on each trial by the computer. C: Voluntary actions with one hand trigger the onset of one tone (e.g., left-hand button press to 900 Hz), with actions from the other hand triggering a different tone (e.g., right-hand button press to 500 Hz).

a concurrent sensory cue, meaning that participants have temporal prediction, temporal control, and non-motor identity prediction but not motor identity prediction because the cue and not their action predicts the identity of the stimulus. In condition type F (see Figure 3C), the participant's action determines which stimulus appears. In this condition, participants additionally have motor identity prediction. This condition thus includes all four processes.

Conditions such as these have been less often used in experimental research on sensory attenuation and intentional binding. However, Table 2 reveals that this group of conditions provides a powerful way to produce contrasts that differ only in terms of one of the four processes. Contrasts C-B and E-D isolate temporal control. Contrasts B-A, E-C, and F-E isolate temporal prediction, non-motor identity prediction, and motor identity prediction, respectively. Note that only contrast F-E can unambiguously demonstrate that intentional binding and sensory attenuation are based on motor identity prediction, which, in turn, would corroborate a major role of forward action models in these perceptual phenomena. If, however, a contrast differs in terms of both motor identity prediction and, say, temporal control (as is the case with contrast 3-2; see Table 1), then we cannot be sure that motor identity prediction truly caused the difference between the conditions. Note also that the conditions and contrasts presented in Table 2 are not exhaustive but are intended to suggest possible ways to isolate the individual processes that contribute to intentional binding and sensory attenuation. One could isolate these processes by contrasting other conditions similar to those presented in Table 2. Our aim in this review is to highlight the importance of using contrasts that isolate these individual processes.

The Role of Predictive Mechanisms in Sensory Attenuation and Intentional Binding

This section evaluates previous experimental data in relation to the processes outlined in the previous section as well as discusses how these processes might lead to the observed effects. Table 3 shows a summary of experimental publications exploring either sensory attenuation or intentional binding. For each experiment, an X is placed below each process that differed in the contrast used in that experiment. That is, the fewer Xs there are, the more precise

the contrast between the conditions used in the given experiment. Table 3 is arranged in clusters of studies. We discuss each of these clusters in turn, beginning with cluster 1, which includes temporal prediction, temporal control, and motor identity prediction. Cluster 2 involves contrasts that exclude temporal prediction but still include temporal control and motor identity prediction. Cluster 3 includes the few studies using contrasts that begin to isolate non-motor identity prediction and motor identity prediction in sensory attenuation or intentional binding. In this way we aim to provide evidence regarding the degree to which these different processes are involved in sensory attenuation and intentional binding.

Cluster 4, discussed at the end, includes those studies that did not contrast any of the processes discussed above (such that there is not a single X in the given line) but that varied other important details, for example, by attempting to manipulate the purported mechanism of action-effect prediction (e.g., Haggard & Whitford, 2004) or by manipulating participants' beliefs regarding the causal role of their action (e.g., Desantis, Roussel, & Waszak, 2011). These additional manipulations are marked in the table where relevant, along with additional task information such as the sensory modality and the dependent variable being measured.

To preview the analysis of the different clusters, we note that some patterns emerge with respect to the likely processes driving sensory attenuation and intentional binding. With regard to sensory attenuation, temporal prediction and temporal control indeed seem to influence the magnitude of attenuation. Nonetheless, preliminary evidence suggests that in addition to these processes, sensory attenuation can be modulated by motor identity prediction. In contrast, intentional binding seems to be largely driven by temporal control and is not modulated by motor identity prediction. Furthermore, both phenomena appear to be strongly influenced by participants' understanding or belief of the causal relationships between their actions and their action effects or between the different sensory events.

Temporal Prediction

Most of the studies in this first cluster are similar to contrast 3-1 (see Table 1). As is evident from Table 3, this contrast results in a difference between the experimental and control

Table 3
Summary of Experiments on Sensory Attenuation (A) and Intentional Binding (B)

Study	Processes				Details				
	Temporal prediction	Temporal control	Non-motor identity prediction	Motor identity prediction	Agency/causal belief	Mechanism	Effect	Sensory modality	Dependent variable
Cluster 1									
Weiskrantz et al. (1971), comparison 1	X	X		X			A	Somatosensory	Self-report ERP (N1)
Schafer & Marcus (1973), comparison 1	X	X		X			A	Auditory and visual	Force judgment
Bays et al. (2005), Groups A and B	X	X		X			A	Somatosensory	MEG (N1m)
Martikainen et al. (2005)	X	X		X			A	Auditory	ERP (N1)
Ford et al. (2001); Ford, Gray, et al. (2007)	X	X		X		✓	A	Auditory	EEG (N1 and beta)
Ford, Roach, et al. (2007)	X	X		X			A	Auditory	PSE
Sato (2008), self vs. control	X	X		X			A	Auditory	ERP (N1/40Hz)
Baess et al. (2008, 2009, 2011)	X	X		X			A	Auditory	
Blakemore et al. (1998); Blakemore, Wolpert, & Frith (1999) ^a	X	X		X		✓	A	Somatosensory	fMRI BOLD
Blakemore, Frith, & Wolpert (1999)	X	X		X			A	Somatosensory	Subjective report
Moore et al. (2010)	X	X		X		✓	B	Somatosensory	Libet clock
Hughes & Waszak (2011)	X	X	X	X		✓	A	Visual	ERP (N2/P3)
Knolle et al. (2012)	X	X		X		✓	A	Visual	ERP (N1)
Cluster 2									
Schafer & Marcus (1973), comparison 2		X		X			A	Auditory and visual	ERP (N1)
Haggard et al. (2002)		X		X			B	Auditory	Libet clock
Haggard & Clark (2003)		X		X			B	Auditory	Libet clock
Sato (2008), other vs. control		X	X	X			A	Auditory	PSE
Wenke et al. (2009)		X ^b		X			B	Auditory	Libet clock
Aliu et al. (2009)		X		X			A	Auditory	ERP (N1)
Cravo et al. (2011)		X		X			B	Auditory	Synchrony judgment
Lange (2011)		X		X			A	Auditory	ERP (N1)
Weiss et al. (2011a, 2011b)		X		X			A	Auditory	PSE
Desantis et al. (2011)		X		X			B	Auditory	Libet clock
Gentsch & Schütz-Bosbach (2011)		X ^c		X		✓	A	Visual	ERP (N1)
Cluster 3									
Baess et al. (2008), predictable vs. unpredictable			X	X			A	Auditory	ERP (N1)
Cardoso-Leite et al. (2010), Experiment 1			X	X			A	Visual	Detection (<i>d'</i>)
Cardoso-Leite et al. (2010), Experiments 2 vs. 1				X			A	Visual	Detection (<i>d'</i>)
Cluster 4									
Haggard & Whitford (2004)						✓	A	Somatosensory	Self-report (of MEP)
Bays et al. (2005), Group C						?	A	Somatosensory	Force judgment
Bays et al. (2006)						?	A	Somatosensory	Force judgment
Voss et al. (2007)						✓	A	Somatosensory	Force reproduction
Buehner & Humphreys (2009)						✓	B	Auditory	Action synchrony task

Note. All the studies in the table reported significant binding or attenuation effects. Processes that differ when comparing the experimental and control task for each study are marked with an X. Additional details include whether the study manipulated or measured causal belief/agency or the mechanism of effect prediction in addition to the sensory modality being examined and the dependent variable. ERP = event-related potentials; MEG = magnetoencephalography; PSE = point of subjective equality; fMRI = functional magnetic resonance imaging. ^a These two papers come from the same data set with an additional regression analysis included in the latter paper. ^b Note that in the externally timed condition participants were required to act within a specified time window but could still vary their action freely within this period. ^c The experimental and control tasks differed with regard to the presence of an action. However, because the actions were stimulus driven, this does not strictly account to a difference in temporal control.

tasks in terms of temporal prediction, temporal control, and action identity prediction. As a consequence, the observed differences between the conditions might be due to any of these processes. However, because subsequent clusters exclude temporal prediction, this first section analyzing Cluster 1 focuses on the way in which temporal prediction (i.e., the ability to predict the point in time at which the stimulus appears) might drive at least part of the observed effects in these experiments (over and above possible effects of temporal control and motor identity prediction). Because, with the exception of one study (Moore et al., 2010, which is discussed in the later section on manipulating action prediction mechanisms), all the experiments in Cluster 1 investigated sensory attenuation, this section focuses on discussing how temporal prediction might affect sensory attenuation. Before discussing how temporal prediction could influence the magnitude of sensory processing, we briefly review the studies in Cluster 1.

We first consider the collection of electroencephalography (EEG) and magnetoencephalography (MEG) studies showing reduced sensory processing of self-triggered compared to externally triggered stimuli (see Figure 2). The majority of these studies used auditory stimuli, either tones (Baess, Horváth, Jacobsen, & Schröger, 2011; Baess et al., 2008; Baess, Widmann, Roye, Schröger, & Jacobsen, 2009; Ford, Gray, Faustman, Roach, & Mathalon 2007; Knolle, Schröger, Baess, & Kotz, 2012; Martikainen et al., 2005; Schafer & Marcus, 1973) or vocalizations (Ford et al., 2001; Ford, Roach, Faustman, & Mathalon, 2007). These experiments typically observe significantly reduced N1 amplitude for action-triggered auditory stimuli measured around 100 ms after the onset of the tone and maximal over central electrodes (see Figure 2C). Fewer experiments have been conducted in the visual domain, with these experiments showing a somewhat less reliable modulation over the vertex (Gentsch & Schütz-Bosbach, 2011; Schafer & Marcus, 1973) or later modulations over frontal and posterior electrodes (Hughes & Waszak, 2011). In each of these studies, the self-generated stimuli were predictable in time (although note that Baess et al., 2008, did include a condition in which they varied the period between the action and the sound), whereas the externally triggered stimuli appeared at unpredictable times.

Other studies in Cluster 1 have reported attenuation of the intensity of tactile self-stimulation (Bays, Wolpert, & Flanagan, 2005; Blakemore, Frith, & Wolpert, 1999; Blakemore et al., 1998; Blakemore, Wolpert, & Frith, 1999). Bays et al. (2005; subject groups A and B; discussed further in a later section) used a combination of a tactile sensor and tactile stimulator to make participants tap on their own finger. They found that such self-administered taps were perceived as attenuated compared to externally triggered taps. In this task, as with the ERP studies described above, temporal prediction is present only in the self-stimulation condition. Blakemore and colleagues (Blakemore, Frith, & Wolpert, 1999; Blakemore et al., 1998) asked participants to control a robotic arm with one hand, which was then used to tickle their other arm. They observed that the greater the delay between the participant's action and the output of the robotic arm, the greater the ticklishness sensation (Blakemore, Frith, & Wolpert, 1999). They also observed increased activity in somatosensory cortex when the robot was controlled by the experimenter rather than the participant

(Blakemore et al., 1998). In these studies, the precise spatio-temporal pattern of movement was predictable only when a participant controlled the robot, and as such the conditions differed in both spatial (in this case, this is synonymous to motor identity prediction) and temporal prediction.

How might such differences in temporal predictability of the stimulus cause sensory attenuation? Some indication could be provided from previous research on temporal attention. Attention has been described as being like a spotlight that amplifies processing (or reduces background noise) where it is shined (e.g., Treisman & Gormican, 1988). Under such an explanation, increased temporal attention toward the stimulus should increase sensory processing and not attenuate it. Indeed, there is much evidence to suggest that when participants' attention is validly cued to a specific point in time, reaction times are significantly reduced (e.g., Coull & Nobre, 1998; for a review, see Correa, Lupianez, Madrid, & Tudela, 2006) and ERP responses are significantly amplified (Correa et al., 2006; Griffin, Miniussi, & Nobre, 2002; Lange, Kramer, & Roder, 2006; Lange, Rosler, & Roder, 2003, although see also Griffin et al., 2002, Experiment 2; Lampar & Lange, 2011; Miniussi, Wilding, Coull, & Nobre, 1999). These findings suggest that rather than producing sensory attenuation, temporal prediction/attention can act in the opposite direction to it by amplifying sensory signals.

However, in certain situations, increased temporal attention has also been seen to significantly attenuate sensory processing. Lange (2009) presented participants with a series of tones that in the baseline condition were presented at regularly spaced intervals (every 550 ms) and increasing or decreasing in pitch, such that both the temporal onset and the frequency of the subsequent tone were predictable (see Figure 4A). In the three other conditions, the temporal sequence (300 to 800 ms), the pitch sequence (randomly ordered pitches), or both were made unpredictable. The penultimate two tones were omitted before participants were presented with the final tone. Thus, in the predictable temporal sequence the time of the final tone was subject to increased temporal attention, whereas the predictable pitch sequence resulted in increased attention toward the identity of the tone. This final tone either was continuous or included a 10-ms gap in the middle. Participants were required either to perform a button press when the gap was present (Experiment 1) or to press one button to signal the presence of the gap and another to signal its absence (Experiment 2). Auditory N1 potentials were significantly reduced in both the temporal prediction and the pitch prediction conditions (see Figure 4B and 4C). This N1 attenuation for both predictable time and predictable pitch is strikingly similar to that observed in ERP studies of sensory attenuation (see Figure 2C). Attenuation of auditory ERPs have also been observed when attention is manipulated by a visual cue. Vroomen and Stekelenburg (2010) presented participants with a ball moving toward a central target (which provides temporal predictability) and measured the ERP response to a crashing sound omitted when the ball and the target collided. They observed an attenuated N1 component compared to a condition without temporal prediction. These studies highlight that when temporal attention is driven by a predictable pattern in a sequence of stimuli, it can lead to a form of sensory attenuation that appears very similar to that observed in a number of the studies in Cluster 1 of Table 3.

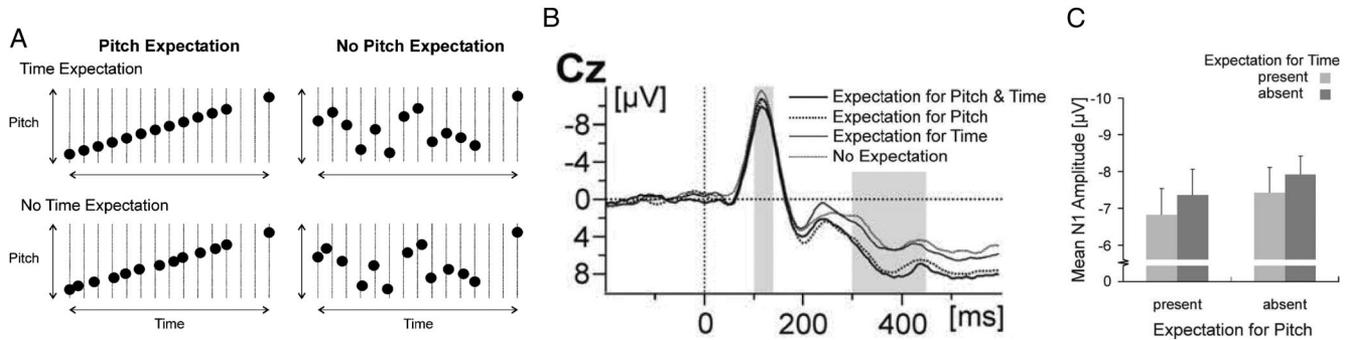


Figure 4. Design and results from Lange (2009). A: Sequences of tones presented followed a predictable pitch and timing (top left), only a predictable timing (top right), only a predictable pitch (bottom left), or neither (bottom right). B and C: Both expectation for pitch and expectation for time resulted in an attenuation of the primary auditory N1 response. From “Brain Correlates of Early Auditory Processing Are Attenuated by Expectations for Time and Pitch,” by K. Lange, 2009, *Brain and Cognition*, 69, pp. 128, 131. Copyright by Elsevier. Reprinted with permission.

Similar paradigms in the visual domain have revealed less clear modulation of sensory processing. Doherty, Rao, Mesulam, and Nobre (2005) employed a methodology similar to Lange (2009). However, rather than playing sequences of tones they presented participants with a ball moving across the screen in either a predictable or an unpredictable manner. They found that increased spatial attention led to a significantly enhanced visual P1 component, with a further enhancement observed with both spatial and temporal attention. In contrast the visual N1 component was significantly reduced for both temporally and spatially predictable stimuli. The P1 modulation was recently replicated by Rohenkohl and Nobre (2011), but they observed no significant modulation of N1 by temporal attention. In relation to the ERP studies in Cluster 1 it is interesting to note that although early sensory modulation is readily observed in auditory tasks (e.g., Aliu et al., 2009; Baess et al., 2008; Martikainen et al., 2005) visual attenuation seems not to affect early components (Hughes & Waszak, 2011), which seems to match well with the results from these temporal attention paradigms. We return to the possible differences across sensory modalities in a later section.

The experiments on temporal attention described above highlight that in some cases increased attention can result in increased sensory processing, while in other cases increased attention can result in sensory attenuation. A number of authors have drawn the distinction between exogenous and endogenous forms of temporal attention (Coull, Frith, Buchel, & Nobre, 2000; Coull & Nobre, 2008; Rohenkohl, Coull, & Nobre 2011), with the former experiments normally considered to be largely driven by endogenous attention and the latter by exogenous attention (Rohenkohl et al., 2011). We do not intend to make any strong claims with regard to whether actions might cue sensory action effects via exogenous or endogenous mechanisms; rather, we simply highlight that under certain circumstances temporal predictability can lead to attenuation of sensory signals independent of any action prediction mechanisms. As such, part of the effects observed in the studies in Cluster 1 might be driven by such temporal prediction mechanisms and not by motor prediction. As discussed below, we suggest that a fruitful way to

overcome these complications when studying sensory attenuation would be to contrast conditions where the sensory event is always cued by an action but the precise relationship between the action and the sensory event is manipulated.

This section outlined the possible role of temporal prediction in the sensory attenuation studies in Cluster 1 of Table 3. Overall, it appears that, particularly for the auditory domain, part of the observed effects might result from this process in sensory attenuation studies that do not control for differences in temporal prediction between the experimental and control tasks. This suggestion is confirmed by those studies that included contrasts in both Cluster 1 and Cluster 2 (Schafer & Marcus, 1973; Weiskrantz et al., 1971). These studies showed that sensory attenuation is reduced when one controls for temporal prediction. Schafer and Marcus (1973) compared stimuli triggered by a voluntary action with the playback of the same stimuli without concurrent action (machine generated) as well as the presentation of periodic stimuli (every 2 s). They found attenuation of both auditory and visual ERP responses over the vertex for self- versus machine-generated stimuli. When they contrasted periodic and self-generated stimuli, however, only auditory potentials were found to be attenuated and to a lesser degree than in the first contrast. The reduced attenuation effect for this contrast, which is equivalent to contrast 3-2 in Table 1, shows that temporal prediction can account for part of the attenuation effect observed in the first cluster of studies in Table 3. Similarly, Weiskrantz et al. (1971) showed that externally administered tickling that was temporally predictable (participants were passively holding the handle of the tickling machine) was deemed as less ticklish than completely externally administered tickling, again suggesting that temporal prediction alone can attenuate sensory processing.

In summary, temporal prediction appears to play an important role in modulating the magnitude of sensory processing and as such likely contributes to the sensory attenuation effects observed in the studies in Cluster 1. Note that studies in this cluster included contrasts that differed not only in terms of motor identity prediction and temporal prediction but also in terms of temporal control. Therefore, even if the effects observed in these studies were not (fully) driven by differences in

temporal prediction, they might still be caused by differences in temporal control, as discussed next, and not by differences in motor identity prediction.

Temporal Control

The previous section discussed those experiments that contrasted conditions differing in, among other processes, temporal prediction. The next cluster of studies in Table 3 (Cluster 2) included a control for temporal prediction but differed in terms of temporal control. Temporal control refers to the presence of an action to allow participants to trigger (or control) the onset of the sensory event. As mentioned above, the studies of Schafer and Marcus (1973) and Weiskrantz et al. (1971) included a control for temporal prediction. Although attenuation effects were reduced when comparing self-administered to externally triggered stimuli, significant attenuation was nonetheless still observed. Other recent studies have confirmed that sensory attenuation still occurs when conditions are matched for temporal predictability either by using periodic stimuli (e.g., Aliu et al., 2009) or by cuing the presentation of externally triggered stimuli (e.g., Lange, 2011). In all these tasks, however (as with all the tasks in Cluster 2), the two conditions still differed not only in terms of motor identity prediction but also in terms of temporal control; that is, the ability for participants to control when the stimulus appeared. This section briefly reviews those studies that utilized contrasts involving temporal control and describes how this process might lead to sensory attenuation and intentional binding.

In addition to the studies described above that compared EEG/MEG responses to action-triggered and externally triggered tones, some studies in Cluster 2 investigated sensory attenuation by

determining the point of subjective equality (PSE) between an action-effect tone and a later comparison tone (Sato, 2008; Weiss, Herwig, & Schütz-Bosbach, 2011a, 2011b). Participants performed voluntary actions that resulted in effect tones of 74 dB. They were then asked to compare the loudness of this tone with that of a second tone that varied from 71 to 77dB. Self-generated tones produced lower PSEs than did externally triggered tones that either were unpredictable in time (Sato, 2008) or were predictable (Weiss, Herwig, & Schütz-Bosbach, 2011a). In all these studies, temporal control was present only for self-generated tones. In a further condition employed by Weiss et al. (2011a), participants could trigger the tone by tapping on the arm of another person, who in turn pressed the button to trigger the tone. Interestingly, they observed significant sensory attenuation in this condition. This condition still differed from the baseline condition in temporal control, albeit indirect temporal control, as the participant’s action triggered the tone via an intermediary.

Cluster 2 also includes a number of studies investigating intentional binding. This phenomenon was first described by Haggard et al. (2002; see also Haggard & Clark, 2003). They asked participants to report—using the Libet clock (Libet et al., 1983)—the timing of action-triggered or externally triggered tones (see Figure 5). In one condition (see Figure 5A) participants performed voluntary actions, which were followed after a short delay (250 ms) by a tone. At the same time they were required to focus on a clock face with a hand rotating at one revolution per 2,560 ms. At the end of each trial participants were asked to report the position of the clock hand either when they performed their action or when they heard the effect tone. This condition was compared with a condition where involuntary muscle twitches were induced by a

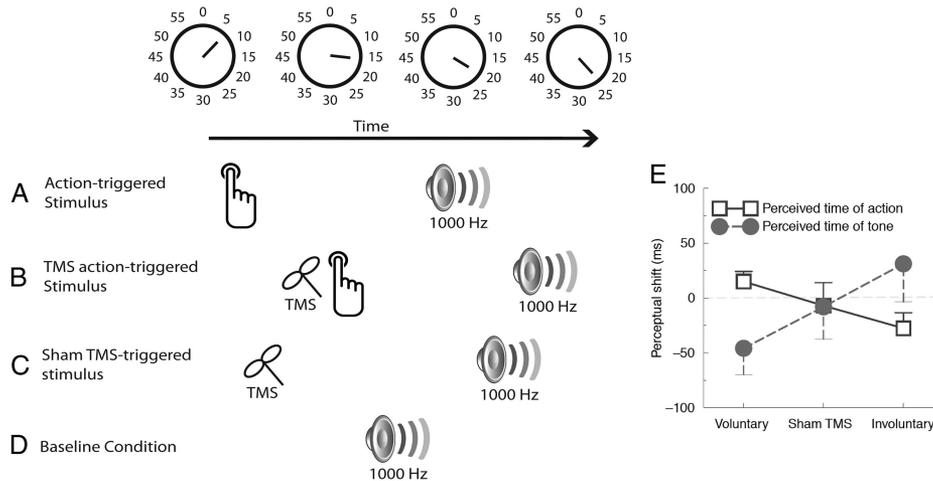


Figure 5. An example of an intentional binding task employed by Haggard et al. (2002). Participants watched a clock face revolve on the screen while they performed actions and heard tones. In A, the tones were triggered (with a delay of 250 ms) by participants’ self-paced voluntary actions. In B, transcranial magnetic stimulation (TMS) to primary motor cortex elicited an immediate muscle twitch and also triggered the effect tone with a delay of 250 ms. In C, TMS was applied but no muscle twitch was elicited. Nonetheless, the tone reliably followed (with a 250-ms delay) the TMS click. In D, participants passively listened to tones presented at random times. Significant binding was observed in the voluntary action condition only (E), with a reverse binding observed for the TMS action-triggered condition. Panel E is from “Voluntary Action and Conscious Awareness,” by P. Haggard, S. Clark, and J. Kalogeras, 2002, *Nature Neuroscience*, 5, p. 383. Copyright 2002 by Nature Publishing Group. Reprinted with permission.

transcranial magnetic stimulation (TMS) pulse (see Figure 5B) and a third condition where a sham TMS pulse was administered and did not result in an involuntary muscle twitch (see Figure 5C). In each of these two conditions the effect tone was triggered by the TMS pulse (with a delay of 250 ms). Haggard et al. observed that action-triggered tones were significantly “bound” in time toward the action, such that compared to a baseline condition where the tone was presented alone (see Figure 5D), the effect tone was perceived to be significantly earlier when it followed a voluntary action (see Figure 5E). In contrast in the involuntary muscle-twitch condition the tone was perceived as significantly delayed, with the sham TMS condition falling between the other two conditions. The comparison between voluntary action and the two TMS conditions, in terms of our processes, reflects a difference in temporal control and motor identity prediction. A further important difference between these conditions is the possible role of causality. Only in the voluntary action condition did participants’ action cause the effect tone. In the involuntary action condition the tone was caused by the TMS pulse and not by the muscle twitch. We return to a discussion of how such difference in causality may influence binding in a later section.

Cravo et al. (2011) measured the perceived time of auditory stimuli by asking participants to rate whether a flash occurred at the same time as a tone. They found that the stimuli were perceived as significantly earlier only when participants controlled the timing of the tone by their action. As with the other studies described above, it is not clear whether the shift in the perceived timing was driven by motor identity prediction or merely by temporal control.

As highlighted by the contrasts in Table 3, for the studies in Cluster 2 the experimental task and control task differed in terms of temporal control as well as motor identity prediction. Before discussing the ways in which temporal control might influence sensory attenuation and binding, we briefly discuss the potential problems with how the studies in this cluster control for temporal prediction. First, it is important to consider how temporal cues might differ from actions in the way they orient temporal attention toward the sensory event. The studies in this cluster controlled for temporal attention either by including a visual cue at the moment where the action occurred in the action condition (e.g., Cravo et al., 2011; Lange, 2011) or by having stimuli appear at fixed intervals. As discussed in the previous section, although some forms of temporal cuing can increase sensory processing, others can lead to sensory attenuation. As such, if the way in which attention is cued differs between the action-triggered stimulus condition and the externally triggered stimulus condition, this might not adequately overcome the potential differences caused by temporal attention. In addition, in those experiments that presented sensory events periodically in the control condition (e.g., Aliu et al., 2009; Schafer & Marcus, 1973), the interval between them was typically fixed at 2 s. In this instance, although the onset is predictable, temporal prediction is likely more accurate when the cue is in close temporal proximity to the stimulus, and thus temporal prediction over a period of 2 s may be less efficient than when the stimulus appears immediately (or soon) after action onset. Possible support for this suggestion comes from the foreperiod paradigm (for a review, see Niemi & Näätänen, 1981), where reaction times are reduced for shorter foreperiods due to the fact that participants can more easily predict the timing of the stimulus at shorter intervals.

In what other ways might temporal control—that is, the presence of an action to control the onset of the stimulus—contribute to the sensory attenuation and intentional binding in the studies described in this section? First, it is important to consider that when a stimulus is externally cued, the cue itself is not temporally predictable. This is in contrast to the action condition, where the cuing of the action effect (by the participant’s action) is predictable in time, as participants can plan when to perform their action. The unpredictable cue in the control condition may in itself produce an orienting response (which is absent in the motor condition) that could, in turn, influence processing of the sensory event (the action effect). Moreover, temporal control may also allow participants to focus attention and reduce distraction even before triggering the stimulus event. If it is the case that participants’ attention is drawn toward the cue for the externally triggered stimuli more than toward the action for action-triggered stimuli, then this should reduce sensory processing in the externally triggered condition, because participants are more distracted in this condition. However, one could also envisage the opposite scenario, such that when participants perform voluntary actions this increases task demands (compared to passively processing a sensory event), because performing a self-paced action requires an internal decision regarding the timing of the action (cf. Lau, Rogers, Haggard, & Passingham, 2004). This increase in task demand could act both to reduce sensory processing (thus causing sensory attention) and to attract attention toward the action, which could in turn draw the action effect closer in time to the action (intentional binding). Note that it is difficult to precisely determine the way in which the presence of an action to trigger a sensory event (temporal control) might influence attention and sensory processing. Nonetheless, it is clear that one can postulate a number of different scenarios that do not require an explanation based on action prediction mechanisms but merely one based on attention-related processes.

A further important consideration is that in the EEG and MEG studies comparing action-triggered tones and externally triggered stimuli (e.g., Baess et al., 2008, 2009, 2011; Hughes & Waszak, 2011; Martikainen et al., 2005), the presence of motor potentials for the action-to-effect condition and not for the effect-only condition may also be problematic. One way to attempt to overcome this problem is to include a motor-only condition to record the participants’ average motor-related potential and then remove this activity from the action to effect grand average (e.g., Martikainen et al., 2005). However, in some cases such a control was not employed (e.g., Aliu et al., 2009) or was not included in the statistical analysis (e.g., Baess et al., 2008). Furthermore, even where such a subtraction of action-related activity is employed, the action-only condition is normally collected in a separate block such that participants know that their action will not trigger an effect. Given that attention demands are different in such blocks and also that motor-related activity may differ when an action effect is predicted (e.g., Hughes & Waszak, 2011), subtracting the motor-only condition may not completely overcome the difficulty of comparing ERP responses to externally triggered versus action-triggered stimuli.

This section described the second cluster of studies in Table 3 that included a control for temporal prediction. The perseverance of both sensory attenuation and binding effects in these experiments suggests that other processes over and above temporal prediction contribute to these phenomena. Nonetheless, the con-

trasts employed in these studies typically differed with regard to both temporal control and motor identity prediction. As discussed above, there are a number of important methodological and technical issues in contrasting conditions that differ with regard to the presence of an action. As we discuss in the subsequent sections, the best way to overcome this might be to systematically vary the relationship between the action and the action effect rather than to compare conditions that include an action with those that involve no action.

It is also important to note that temporal prediction and temporal control might interact with one another. A number of studies have found that binding and attenuation can occur in the absence of precise temporal prediction, as long as temporal control is present. Haggard et al. (2002; Experiment 2) found that although binding was reduced for blocks containing mixed stimulus onset asynchronies (SOA) between action and effect, it was not abolished. With regard to sensory attenuation, Aliu et al. (2009) showed that when participants were trained on blocks with a 100-ms delay between their action and the effect tone, sensory attenuation still occurred in a block of trials where the action-to-effect SOA was randomly either 0 ms or 200 ms. Similarly, Lange (2011) showed that sensory attenuation occurred even in blocks with a random delay between the action and the effect tone. These findings might appear contradictory with respect to the experiments described earlier, which showed that temporal attention alone can produce attenuation effects similar to those typically attributed to action-effect prediction. One possible explanation is that temporal prediction or temporal control alone might be sufficient to produce attenuation and that their combination simply serves to magnify the effect. This suggestion is consistent with those studies that have shown a reduced attenuation effect when controlling for temporal prediction (e.g., Schafer & Marcus, 1973; Weiskrantz et al., 1971). Employing contrasts such as B-A, C-B, and E-D (see Table 2) might help to elucidate the unique contribution of each of these processes to intentional binding and sensory attenuation.

Up to this point we have considered the possible influence of temporal prediction and temporal control on intentional binding and sensory attenuation. All studies in Clusters 1 and 2 differed in terms of motor identity prediction and also with regard to temporal control and/or temporal prediction. The evidence reviewed above showing that temporal attention can influence early sensory processing is particularly important for studies of sensory attenuation, which often contrast conditions that differ with regard to this process. Temporal control, as achieved by the presence of a voluntary action to trigger the stimulus, may contribute to effects observed in previously published accounts of both intentional binding and sensory attenuation. Furthermore, the precise interactions between these different processes and the ways in which temporal attention may be cued differentially by different events is unclear, making isolation of the precise effect of these processes difficult to assess using the contrasts outlined in Table 1 and utilized by the studies in Clusters 1 and 2 of Table 3. We now turn to the most important question: Does identity prediction result in sensory attenuation or intentional binding?

Non-Motor Identity Prediction and Motor Identity Prediction

We draw a distinction between identity prediction that results from choosing between two possible actions (motor identity pre-

dition) and prediction of the identity of the stimulus that is not dependent on which specific action is performed but that results from a predictive cue (non-motor identity prediction). To look ahead briefly, a dissociation between intentional binding and sensory attenuation emerges. Although some evidence suggests that sensory attenuation is modulated by motor identity prediction, intentional binding might rather be the product of temporal control.

If sensory attenuation and intentional binding effects are the result of predictive action mechanisms (e.g., see Figure 1), they should be observed for contrasts isolating identity prediction. Furthermore, if these predictive mechanisms are specific to the action system, they should also be observed in a contrast isolating motor identity prediction. To our knowledge, few experiments have utilized such contrasts. In an experiment investigating sensory attenuation, Baess et al. (2008) included a condition where the identity of the action-triggered tone was predictable (1,000 Hz) and compared this with action-triggered tones of an unpredictable identity (400 to 1,990 Hz). They found significantly attenuated N1 amplitude in the predictable condition compared to the unpredictable condition, suggesting that knowledge of the identity of the action effect increases sensory attenuation. No significant modulation of N1 amplitude was observed for externally triggered tones with predictable versus unpredictable identity (non-motor identity prediction), although this did approach significance. Note, however, that the non-motor identity prediction condition also differed in terms of temporal prediction and temporal control; thus, the precise interaction between these processes is difficult to assess in this comparison. Nonetheless, this finding provides initial evidence that action identity prediction can drive sensory attenuation.

Further evidence in support of this conclusion comes from a study by Cardoso-Leite et al. (2010). They trained participants to associate left- and right-hand movements with Gabor patches of different orientations. In the test phase, participants were presented with near-threshold Gabor patches whose orientations were either congruent or incongruent with their learned action effect contingencies. On half the trials no patch was presented, and participants were required to determine on each trial whether a Gabor patch was presented or not. Perceptual sensitivity (measured by d') was significantly lower in the congruent condition. This study provides evidence that the realization or violation of hand-specific predicted action effects influences visual sensitivity. To check that these effects were caused by action prediction and not caused by non-motor identity prediction, Cardoso-Leite et al. employed a further control task. In this task participants pressed the two buttons at the same time and heard a concurrent sound. The frequency of this sound predicted which of the two orientations would be presented. As with the previous task, participants first acquired the relevant mappings and were then tested in a visual detection task using congruent and incongruent trials. In this task, the Gabor orientation could be predicted with 100% accuracy by the tones, as in the action condition, but now the action simply served to trigger the tone and not to determine its identity. Sensitivity was not different for congruent or incongruent trials in the tone prediction task, confirming that non-motor identity prediction did not drive the difference in the action prediction condition. Thus, this finding shows that action prediction mechanisms can reduce visual sensitivity over and above any effects of temporal prediction, temporal control, and non-motor identity prediction. The contrast between the main experiment and the control experiment is equivalent to

contrast F-E in Table 1 and as such isolated only motor identity prediction.

Similar effects have been observed in experiments investigating chromatic adaptations to eye movements as well as other actions (Bompas & O'Regan, 2006a, 2006b; Richters & Eskew, 2009). Richters and Eskew, for example, associated participants' left and right eye movements to a red or green stimulus, respectively. Following this training phase, participants' PSE for two color stimuli presented immediately after the eye movements were shifted, showing that participants' prediction influenced their sensory experience of the stimulus. Richters and Eskew also conducted control experiments similar to the one employed by Cardoso-Leite et al. (2010), to show that these adaptations did not occur when tones rather than actions were associated with particular colors. Furthermore, Richters (2008) observed the same effect when associating leftward movements of a joystick with the presentation of a red stimulus and rightward movements with that of a green stimulus, demonstrating that the mechanism producing the effect is of a general nature and not restricted to eye movements.

This lack of an effect in the control experiments of Richters and Eskew (2009) and Cardoso-Leite et al. (2010) raises a further interesting issue. In the temporal attention task by Lange (2009), described above, a significant attenuation of the auditory N1 was observed both when the stimulus was temporally predictable and when the tone was predictable. This finding suggests that non-motor identity prediction, in this case the frequency of the tone, can lead to sensory attenuation in the absence of any action (see also Vroomen & Stekelenburg, 2010). This appears inconsistent with the result in the control tasks described above. One possible way to reconcile the difference between these results is that in the studies by Lange (2009) and Vroomen and Stekelenburg (2010) the prediction of the frequency of the target tone developed over time, as the sequence of tones increased or decreased in a predictable fashion. This means that after only a few tones in the sequence of 12 tones, participants could begin to form a prediction regarding the pitch of the final tone in the sequence, whereas in the non-motor identity prediction condition employed by Cardoso-Leite et al. (2010) the prediction was available only once the participant had already pressed the button. In contrast, the temporal development of identity prediction in the action prediction task is more similar to that in the task by Lange, such that participants begin to prepare their action in advance, with this increased action preparation increasing the expectation that one stimulus will be presented.

If, as the results from Lange (2009) and Vroomen and Stekelenburg (2010) suggest, sensory attenuation can occur in the absence of any action, this might point toward the possibility that the predictive mechanisms involved in the phenomenon are not limited to action prediction. Indeed, predictive mechanisms have been recently invoked to understand another attenuation phenomenon, that of repetition suppression (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Repetition suppression refers to the fact that repeated presentation of the same stimulus results in a reduction of the neuronal response to the stimulus (Grill-Spector, Henson, & Martin, 2006; Miller, Li, & Desimone, 1991). Summerfield et al. found that repetition suppression was greater when the probability of repetitions was high (75%) than when it was low (25%), suggesting that attenuation of the neuronal responses in repetition suppression is driven by increased expectancy of the stimulus. Todorovic, van Ede, Maris, and de Lange (2011) ob-

served a similar modulation of evoked MEG responses and gamma band synchrony, such that repetition suppression was smaller for unpredictable auditory stimuli. Further evidence that prediction can lead to attenuation of the neural processing of visual stimuli independent of action comes from a study by Egner, Monti, and Summerfield (2010), who found that the difference in activity for faces compared to houses in fusiform face area was greater for unpredicted face stimuli than for situations when there was a high probability of a face stimulus.

These experiments highlight that prediction is strongly utilized outside the motor system. It might also be possible that such non-motor predictions harness the predictive nature of the action system. Evidence in favor of such a possibility comes from Schubotz and von Cramon (2002). They found that, in the absence of motor preparation, the prediction of stimulus size involves the superior part of the ventrolateral pre-motor cortex, with prediction of the tone of a pitch occurring in the inferiormost ventrolateral premotor cortex. They suggest that predictions of events are mapped on to somatotopically organized motor schemas. A detailed discussion of the interrelation between action prediction mechanisms and more general prediction mechanisms is beyond the scope of the current review (for a recent review, see Bubic, von Cramon, & Schubotz, 2010). These studies nonetheless highlight that predictive mechanisms extend beyond forward action models. Comparing non-motor identity prediction and motor identity prediction may help one to determine whether action prediction utilizes the same mechanisms as other forms of sensory prediction, perhaps with greater efficiency, or whether differences in the magnitude of these different predictive mechanisms on intentional binding and sensory attenuation may rather reflect the temporal dynamics intrinsic to prediction involved in voluntary action selection.

In assessing such differences it will also be of crucial importance to ensure that any control condition predicts the sensory event of interest in a similar way to the prediction afforded by selecting an action. For instance, although the study from Cardoso-Leite et al. (2010) showed that a Gabor patch whose identity is predicted by a tone does not show the same attenuation as the same patch correctly predicted by an action, it is important to consider other ways in which these two conditions differ. In the action prediction condition, the action might be considered task relevant, because on each trial participants are required to choose which action to perform. In contrast, in the control condition, the predictive tone is not task relevant but simply occurs in synchrony with another, nonpredictive, action. This reduced task relevance may lead to a reduced prediction, which could in turn lead to a reduced (or absent) attenuation effect. Therefore, even when one uses the contrasts that should, in theory, isolate action prediction mechanisms, additional difference may remain that could account for the presence or absence of sensory attenuation. As such, these contrasts could be described as necessary to show that action prediction drives these phenomena, but they still might not be sufficient. In addition, utilizing lengthy association phases, as well as testing for the presence of an association between the predicting stimulus and the predicted stimulus, might help to ensure that the lack of an effect in the control task is not driven by the absence of a well-learned association.

In the first part of this section on identity prediction we discussed evidence that sensory attenuation can result from identity specific action-effect predictions (motor identity prediction). This

provides preliminary evidence that sensory attenuation is the result of forward prediction mechanisms. We now turn our attention to the question of whether intentional binding might be modulated motor identity prediction. We (Desantis, Hughes, & Waszak, 2012) employed contrasts similar to those employed by Cardoso-Leite et al. (2010) to examine the degree to which motor identity prediction influences measures of binding. In Experiment 1, participants performed a left- or right-hand button press to trigger a sound 450 ms after action onset. In one condition the participants' button press (left or right) predicted which of two tones would be presented. In the other action condition the tone of the action effect was randomly selected and was therefore independent of which button the participant pressed. In the control condition, the action was replaced by another sound (tone-to-tone condition). We found significant binding in both action conditions compared to the control condition. However, we found no significant difference between our two action conditions, suggesting that the magnitude of the binding effect was independent of motor identity prediction mechanisms. In a second experiment, we tested whether binding was reduced when the motor identity prediction was violated. Again, we observed significant binding, but this did not differ between valid and invalid trials, suggesting that accurate motor identity prediction was not necessary to produce intentional binding. Haering and Kiesel (2011) employed a similar paradigm to measure intentional binding to validly or invalidly predicted action-effect tones as well as visual stimuli. In each of four experiments they observed the normal binding effect using both time estimation and Libet clock methods. However, the magnitude of the binding effect was not influenced by the validity of the action-effect prediction, independent of which method was employed, which modality was tested, the percentage of valid trials, and the action-effect interval. All these results point toward the possibility that although motor identity prediction modulates sensory attention, binding may be driven by differences in temporal control.

To sum up, our analysis revealed that although intentional binding appears not to vary dependent on the validity of an action-specific prediction, preliminary evidence suggests that sensory attenuation is modulated by motor identity prediction. Indeed, recent years have seen a significant increase in interest in how predictions guide our perception of events in the external world (cf. Bar, 2011). Utilizing the rigorous comparisons between different processes outlined in Table 2 should help to further distinguish motor identity prediction from other forms of prediction and to show more generally how prediction impacts on sensory processing.

In the subsequent sections we briefly discuss how combining the approach described above with neuroimaging methods will be important in further linking motor prediction with sensory attenuation and intentional binding. In the following section we discuss the possible role of causal belief in these phenomena and how they influence the feeling of agency, both when it is functioning normally and when it goes wrong, as in the case of schizophrenia.

Manipulating and Measuring the Mechanisms of Attenuation and Binding

The final cluster of studies in Table 3 do not compare any of the processes examined above but manipulate either causal belief or the purported mechanism of action-effect prediction. This section briefly describes those studies in Table 3 that include a tick to

show that they have directly measured or manipulated activity in the human motor cortex to investigate mechanisms of binding or attenuation (for a related review, see Waszak et al., 2012). For example, Haggard and Whitford (2004) found that a TMS-induced muscle twitch was rated as being smaller when it occurred alongside a concurrent voluntary action. On some trials, a TMS pre-pulse was administered over supplementary motor area (SMA) 10 ms prior to the pulse producing the test motor-evoked potential. This pre-pulse almost abolished the sensory attenuation produced by the voluntary actions. Haggard and Whitford suggested that applying a pre-pulse to SMA immediately prior to action onset disrupts the generation of a motor efference copy that drives sensory attenuation. Pre-SMA has also been shown to be involved in predictive mechanisms in binding. Moore et al. (2010) found that TMS theta burst disruption of activity in pre-SMA and not in control areas resulted in significantly reduced binding of the action effect toward the action. This finding may appear in contrast to the results described above, which suggest that intentional binding is driven not by motor prediction but by temporal control. However, the precise mechanism by which temporal control might cause intentional binding remains to be determined. Because temporal control involves action triggering of a stimulus, this may still involve the action system in some way even if binding is not driven by motor identity prediction.

Recently, Hughes and Waszak (2011) compared movement-related motor potentials in human EEG for voluntary actions that were associated with an effect and those that were not. They predicted that if the efference copy is generated in SMA, they should observe a difference in the readiness potential (RP) between actions that were associated with an effect and those that were not. However, rather than finding a difference in RP, they found differences in the lateralized readiness potential (LRP; Coles, 1989; Kutas & Donchin, 1980), which is normally assumed to be generated in primary motor cortex (Coles, 1989; Leuthold & Jentzsch, 2002). Thus they argued that primary motor cortex is involved in predicting whether or not a hand-specific movement would result in a predictable sensory consequence. This suggestion is consistent with a study by Voss, Bays, Rothwell, and Wolpert (2007), who showed that theta burst stimulation of primary motor cortex resulted in reduced overestimation of the force required to replicate a tap to their own hand in a force reproduction task.

Blakemore et al. (1998) employed a similar contrast in a study where participants' finger movements resulted in tactile stimulation of the other hand (discussed in detail above). They found that activity in right anterior cerebellar cortex was increased in the action-to-effect condition compared to the action-only condition. Furthermore, this activation was correlated with the reduced activity in somatosensory cortex in response to self-administered tickling (Blakemore, Wolpert, & Frith, 1999). These results suggest that as well as SMA and primary motor cortex, cerebellum is involved in predictive processes that alter the perception of the effect of one's action. Further support for the role of the cerebellum in sensory attenuation comes from a recent study by Knolle et al. (2012), who showed that N1 attenuation of action-triggered tones is reduced in patients with cerebellar lesions. A correlation between pre-action EEG activity and sensory attenuation was also reported by Ford, Roach, et al. (2007). They observed a significant correlation between intertrial coherence in the beta band prior to vocalizations and attenuation of the N1 auditory ERP to the sound

of the vocalization. Moreover, both the pre-action beta synchrony and the correlation between synchrony and N1 were absent in a sample of patients with schizophrenia, consistent with the suggestion that this population has problems with agency attribution (Franck et al., 2001).

These experiments provide evidence that activity in the motor system is involved in phenomena such as sensory attenuation and binding and that disrupting activity in these areas results in a reduction of these effects. However, it is important to note that although these studies show an association between the motor system and these phenomena, they do not provide direct evidence that motor prediction drives the effects. As discussed above, the motor system may also be involved in making nonmotor predictions (e.g., Schubotz & von Cramon, 2002). By combining these techniques with the conditions and contrasts outlined in Table 2 one might be able to further determine the precise brain mechanisms involved in motor and nonmotor identity prediction.

The Role of Agency and Causal Belief

A number of studies in Table 3 also measured or manipulated agency or causal belief. We define agency as the attribution of having caused something, for example, that an external event is caused by oneself (e.g., Gallagher, 2000). Causal belief is closely linked to agency but can also refer to the perceived causal links between two events in the environment that may not involve an agent (e.g., Scholl & Tremoulet, 2000). These studies described in this section typically manipulated participants' prior belief about the relationship between an action and an effect. Desantis et al. (2011), for example, showed that the shift in the perceived time of the action effect was abolished when participants were led to believe that an action effect was caused not by them but by a confederate acting as another subject (see Figure 6). This was despite the fact that the sound was always triggered by the participants' button press. This shows that beliefs regarding the causal link between the action and the effect can influence the degree of intentional binding. Desantis et al. took their finding to indicate that prior authorship belief affects predictive mechanisms, for example, by determining how reliable the cognitive system considers predictive signals to be or whether or not a predictive signal is computed in the first place. A number of other studies have also highlighted the importance of causal belief in intentional binding (Buehner & Humphreys, 2009; Ebert & Wegner, 2010; Humphreys & Buehner, 2009, 2010; Moore, Wegner, & Haggard, 2009; Obhi & Hall, 2011). Although these studies are not included in Table 3 because they did not independently measure the perceived timing of the action and the action effect, these findings are in line with those described above (Desantis et al., 2011). Indeed, a spatial equivalent of intentional binding has been observed to vary dependent of perceived causality and completely independent of an action (Buehner & Humphreys, 2010). Thus, Buehner and Humphreys suggested that the phenomenon be called causal binding and not intentional binding, as it appears to extend to all situations where causality can be inferred and not only to intentional action.

A number of studies in Table 3 include a question mark under the causal belief mechanism. The conditions in these studies appear not to be differentiable by any of the four processes but might be explained in terms of the belief of participants that their action caused the somatosensory effect. These experiments used a para-

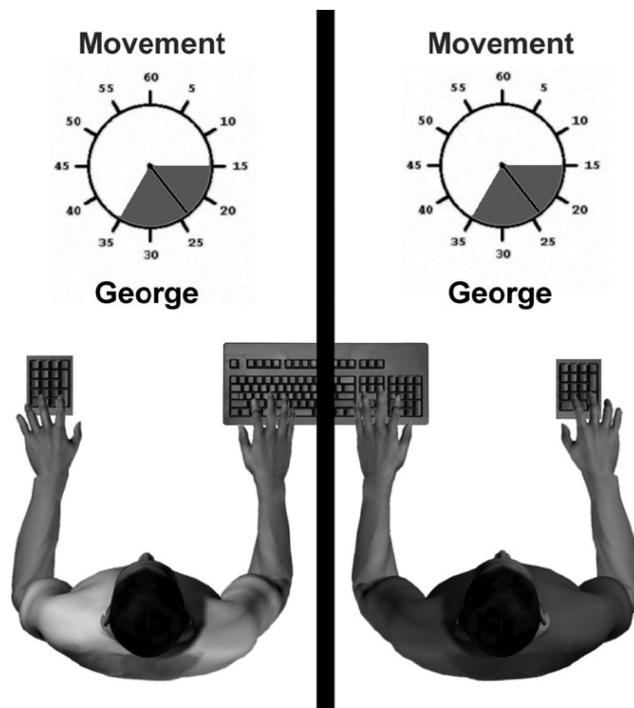


Figure 6. Illustration of the experimental setup from Desantis et al. (2011). The experiment included both a real participant (on the left) and a confederate (on the right). They were separated by a piece of cardboard and shared one keyboard to trigger the sounds. They saw the same stimuli on the screens. Participants were required to perform keypresses when the clock hand was in the highlighted area of the clock. The instruction above the clock informed them of whether to report the time of their movement or the time of the action-effect tone, which they reported at the end of each trial. The name of the participant whose action would supposedly trigger the tone was presented below the clock. Participants were asked to press a button even when the screen told them that their action did not trigger the sound. In fact, all action effects were triggered by the real participant and not by the confederate. The perceived timing of the action effect was shifted only when participants believed that their action triggered the tone. From "On the Influence of Causal Beliefs on the Feeling of Agency," by A. Desantis, C. Roussel, and F. Waszak, 2011, *Consciousness and Cognition*, 20, p. 1215. Copyright by Elsevier. Reprinted with permission.

digm similar to that originally employed by Bays et al. (2005), discussed above. In the Bays et al. experiment, participants rested their left hand under a force sensor fixed to a torque motor. Participants tapped the top of the force sensor with their right hand, which resulted in (with a variable delay of -300 to 300 ms) stimulation of their left hand via the torque motor. The negative delays were achieved by calculating the participants' mean reaction time (RT) to the go signal and then presenting the tap at this mean RT minus the delay following the go signal. Participants were asked to rate the intensity of the stimulation compared to a reference stimulation that occurred 800 to 1,500 ms later. Participants rated the stimulation as significantly reduced in comparison to a condition with no action, with the greatest attenuation when the stimulation occurred in synchrony with the tap. As discussed above, for Groups A and B the conditions differed in temporal prediction because in the no-action condition participants could

not predict the timing of the stimulation. For Group C a number of additional conditions were included. In one condition, participants were instructed to stop just before touching the sensor, at which point the motor was employed to stimulate the left hand. In another condition they were told to perform the tapping action but to deliberately miss the sensor. Interestingly, although participants' action always resulted in stimulation in these conditions, no sensory attenuation was observed.

Bays, Flanagan, and Wolpert (2006) employed a similar paradigm but fixed the participants' right hand to allow only a flexion of the finger to tap the sensor. On one sixth of all trials the sensor unexpectedly moved before participants could make contact, but the stimulation occurred at the point at which their finger would have touched the sensor. In this instance sensory attenuation occurred despite the absence of contact. Bays et al. suggested that this provided evidence that attenuation relied on predictive mechanisms, as participants could not predict when the sensor would be moved away and therefore programmed their action with the expectation that it would produce a stimulation on their left hand. In a second experiment the sensor was moved on every trial, such that contact was never made. In this instance no attenuation was observed, as participants would not predict contact to be made with the sensor. Again, this finding is perhaps somewhat surprising in the context of many other studies on sensory attenuation, because on every trial participants performed an action that resulted in sensory stimulation of their other hand in an entirely predictable manner, yet no attenuation was present. One possible explanation would be that although the action reliably caused the effect, the causality of their action to the effect was not well established. Given the experimental setup, in which the sensor was placed directly above the other hand, and participants' knowledge that a tap on the sensor results in stimulation of the other hand, the causal relationship is very clear. However, when participants deliberately miss the sensor, the causal link is less clear. In many other experiments the association between the action and effect was more abstract, such that a button press produces a tone or a visual stimulus. Such experiments typically employ an acquisition phase to build up the action effect association and to reinforce the causal link between action and effect. Perhaps the lack of an acquisition phase for the experiments by Bays et al. means that, unless their action has a clear causal link to the action effect, participants do not build a causal association between the action and the effect.

The studies discussed in this section show that over and above the different processes described, participants' causal beliefs play an important part in intentional binding and sensory attenuation. As suggested by Desantis et al. (2011), this might reflect the fact that participants put more weight on their prediction if they believe that a causal link exists between action and effect, or it might reflect the fact that participants do not predict the action effect at all if they believe that the sensory event is unrelated to their action. Another possible explanation could be that prior belief may guide sensory motor learning by preventing or facilitating the acquisition of new action-effect associations. Indeed, the precise mechanism by which causal belief influences sensory attenuation and intentional binding requires further clarification. The studies reviewed in this section serve to highlight the importance of causal belief in these phenomena. However, it is not clear which process causal belief influences. For example, increased perceived causality may lead to improved temporal attention by making the relationship

between the stimuli more salient. Causality might rather influence identity prediction mechanisms by increasing the strength of these predictions. Another possibility is that causal belief does not strengthen prediction but is an additional independent factor driving attenuation and binding. Indeed, because preliminary evidence suggests that intentional binding is driven not by motor prediction but by temporal control and because agency has been seen to modulate binding, causal belief must act independently to action prediction mechanisms, at least in the generation of binding. By examining the types of contrasts outlined in Table 2 while at the same time varying the causal relationship between the predicting and predicted event, future research will help to determine precisely how causal belief interacts with prediction mechanisms.

Binding and Attenuation as Measures of Action Prediction and Agency

The previous section discussed how causal belief and agency belief can influence the magnitude of intentional binding. However, these phenomena are also often cited as objective measures of agency, in that binding and attenuation are the mechanisms by which we judge the causality of events (e.g., Gentsch & Schütz-Bosbach, 2011; Haggard et al., 2002). Because the framework presented in this review questions the precise mechanisms that drive sensory attenuation and intentional binding, this may have important implications for the way in which both these phenomena are used to assess disorders of action prediction and agency, such as delusions of control and hallucinations in patients with schizophrenia. For example, sensory attenuation—as measured by comparing self- and externally generated stimuli—has been widely advocated as a tool for assessing maladaptive efference copy generation in schizophrenia (e.g., Ford, Gray, et al., 2007; Ford et al., 2001; Ford, Roach, et al., 2007; Ford, Roach, & Mathalon, 2010). However, if as suggested above, such contrasts are confounded by differences in temporal prediction, the reduction in N1 attenuation observed in schizophrenia may be more symptomatic of deficient attentional processing than action prediction mechanisms. Other attenuation paradigms have also been utilized to test for the same purported forward action mechanism deficit in schizophrenia (e.g., Shergill, Samson, Bays, Frith, & Wolpert, 2005). However, as outlined above these different paradigms appear to be based on somewhat different mechanisms, leaving the underlying cause of the prediction disorder in schizophrenia unclear.

Similarly, intentional binding has been observed to be reduced in patients with schizophrenia (e.g., Voss et al., 2010). This finding is often reported to be a possible basis for misattribution of agency in this group that ultimately feeds into delusional beliefs (e.g., Fletcher & Frith, 2009; Frith, Blakemore, & Wolpert, 2000). Our evidence reviewed above suggests that forward model based action systems might not contribute to intentional binding, but rather that intentional binding is largely the result of temporal control. That is not to say that the binding observed in such paradigms is not in some way related to agency attribution, but that it might not be directly related to action prediction mechanisms as has previously been assumed. Applying a framework similar to that outlined in this review would help to determine the precise deficit in patients with schizophrenia.

Further Outstanding Issues

Another important aspect of binding and sensory attenuation that requires further clarification is the possible similarities and differences between the effects observed in different sensory modalities. For example, most ERP studies of sensory attenuation in the auditory domain observed an early difference over frontocentral electrodes (e.g., Aliu et al., 2009; Baess et al., 2008; Martikainen et al., 2005), presumed to reflect modulation of the N1 sensory auditory component. However, results in the visual domain point to the possibility that this activity may not be specific to auditory tasks and as such may not reflect primary sensory processing (Gentsch & Schütz-Bosbach, 2011; Hughes & Waszak, 2011; Schafer & Marcus, 1973). This might be partly related to the effects described above in some temporal attention tasks, where auditory ERPs have typically been seen to be attenuated for validly cued stimuli (Lange, 2009; Vroomen & Stekelenburg, 2010) and in some cases early visual ERPs are increased (e.g., Rohenkohl & Nobre, 2011). To the best of our knowledge only one ERP study has investigated auditory and visual sensory attenuation in parallel (Schafer & Marcus, 1973), and it found modulations of frontocentral components for both auditory and visual stimuli. By employing the contrasts proposed in this review, future research should attempt to further isolate the degree to which visual and auditory effects overlap and also to determine which specific processes are associated with the observed modulations.

A number of studies investigating sensory attenuation have focused on somatosensory stimuli in addition to visual and auditory research. These studies typically investigate situations in which participants are asked to apply a force to another part of their body, with attenuation effects measured either by subjective report (e.g., Blakemore et al., 1998) or by a force-matching procedure (e.g., Bays et al., 2005, 2006). With reference to the latter effects in particular, these experiments appear to show a somewhat different pattern of results regarding what is sufficient to produce attenuation. For example, many of these conditions in these studies did not result in attenuation effects even though stimulation predictably followed on from their action. As discussed above, this might reflect modulation of causal belief that the action effect is related to the action. Another possibility is that given that somatosensory attenuation is also observed for the moving body part that is performing an action (e.g., Chapman, Bushnell, Miron, Duncan, & Lund, 1987), somatosensory processing may be more tuned to gating mechanisms required to prevent excessive feedback during action execution. Future research should compare somatosensory and visual effects in similar paradigms to attempt to disentangle these two possible explanations.

Summary

This review systematically investigated the conditions that have been compared in previous published accounts of sensory attenuation and intentional binding. We contrasted the control conditions and experimental conditions in these studies to determine which of four processes—temporal prediction, temporal control, non-motor identity prediction, and motor identity prediction—differed in the contrasts they utilized. Our analysis suggests that the sensory attenuation effect observed in the majority of experiments is likely partially caused by a difference in temporal prediction. This pos-

sibility is reinforced by research in temporal attention, which shows that in certain circumstances increased temporal prediction can lead to attenuation of sensory processing. Nonetheless, a number of studies that did control for temporal prediction still reported sensory attenuation and intentional binding, particularly in the auditory and somatosensory domains. However, these studies differed with regard to the presence of an action to trigger the onset of the stimulus (temporal control). As such, these studies were not able to isolate motor identity prediction as the cause of these phenomena.

Only a relatively few studies on sensory attenuation have begun to isolate motor identity prediction mechanisms from temporal prediction and temporal control. For example, Cardoso-Leite et al. (2010) showed that sensory attenuation appears to be sensitive to action-specific prediction mechanisms. However, the precise nature of this mechanism, as well as how it compares to other, more general predictive mechanisms, remains to be clarified. For example, some previous research has shown that identity prediction completely independent of action can result in sensory attenuation (e.g., Lange, 2009; Vroomen & Stekelenburg, 2010).

With regard to intentional binding, previous studies have failed to isolate motor identity prediction from temporal control. Our own data (Desantis et al., 2012) indicate that motor identity prediction mechanisms do not modulate the magnitude of this effect, suggesting that temporal control maybe be sufficient to produce intentional binding. Overall it appears that although sensory attenuation may be modulated by action identity prediction, intentional binding is not. The framework presented here has important implications not only for determining the precise processes that lead to these phenomena in normal functioning but also for assessing which of these processes might lead to the reduction of binding and sensory attenuation observed in patients with schizophrenia.

In addition to assessing the contribution of these four processes to attempt to isolate motor prediction, we reviewed a number of studies that highlight the importance of causality in these phenomena. For example, intentional binding has been observed to be modulated by the degree to which participants believe their action to be the cause of the effect (Desantis et al., 2011). Indeed, perceived causality itself independent of any action has been observed to result in a form of spatial binding (Buehner & Humphreys, 2010). With regard to sensory attenuation, although no studies have directly assessed the role of causality, some evidence in the somatosensory domain points toward the possibility that this phenomenon is also modulated by causality (e.g., Bays et al., 2006).

We further considered the importance of manipulating or measuring activity in the action system in the brain associated with action-effect prediction. Although these studies provide an important tool for assessing the role of action prediction mechanisms in processing of action effects, they could perhaps go one stage further by attempting to correlate the degree to which action systems are engaged on a given trial with the magnitude of sensory attenuation (although see Ford, Roach, et al., 2007). Similarly, measuring these phenomena behaviorally and with functional imaging or electrophysiological recordings would help to test whether the different measures correspond in a single task. We highlighted a number of further important methodological issues and proposed conditions and contrasts that could be utilized to help

determine the role of action prediction mechanisms in sensory attenuation and intentional binding.

In conclusion, in this article we have presented a new framework for assessing the precise mechanisms that drive sensory attenuation and intentional binding and proposed a number of important avenues for future research that will help to clarify the precise way in which attention, motor prediction, and causality interact to alter the perception of the sensory consequences of our actions.

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