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Review

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ABSTRACT

Voluntary actions are thought to be selected with respect to their intended goal. Converging data suggests that medial frontal cortex plays a crucial role in linking actions to their predicted effects. Recent neuroimaging data also suggests that during action selection, the brain pre-activities the representation of the predicted action effect. We review evidence of action effect prediction, both in terms of its neurophysiological basis as well as its functional consequences. By assuming that action preparation includes activation of the predicted sensory consequences of the action, we provide a mechanism to understand sensory attenuation and intentional binding. In this account, sensory attenuation results from more difficult discrimination between the observed action effect and the pre-activation of the predicted effect, as compared to when no (or incorrect) prediction is present. Similarly, a predicted action effect should also reach the threshold of awareness faster (intentional binding), if its perceptual representation is pre-activated. By comparing this potential mechanism to mental imagery and repetition suppression we propose a possible neural basis for the processing of predicted action effects.

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Contents

1.	Ideomotor action	944
2.	Neurophysiology of action outcome anticipation: MFC and cerebellum	944
3.	Neurophysiology of action outcome anticipation: perceptual areas	946
4.	Processing of action effects	948
	4.1. Processing of unanticipated action effects	948
	4.2. Processing of anticipated action effects: sensory attenuation	949
	4.3. Processing of anticipated action effects: chromatic judgments	951
	4.4. Processing of anticipated action effects: intentional binding	951
5.	Anticipation, control, temporal prediction	952
6.	A pre-activation account of sensory attenuation and intentional binding	953
7.	Similarities between action effect anticipation and imagery	955
8.	Repetition suppression as a neural basis of the perceptual consequences of action effect anticipation?	956
9.	Conclusions and outlook	956
	References	957

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Human action serves two complementary purposes: to achieve effects in the environment as a consequence of an internal desire, or to accommodate to environmental demands as a consequence of an external event. The former type of action is usually referred to as "voluntary", "goal-directed", or "intention-based". The latter is often conceptualized as "response", "reaction", or "stimulusbased".

The main focus of research has been on actions performed in response to external stimuli. The history of reaction time

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experiments is as long as the history of experimental psychology itself. Along with psychophysics, reaction time studies were the method of choice in the early experimental laboratories and have been ever since.

The control of intention-based actions, on the other hand, has attracted comparatively little attention (cf. Prinz and Hommel, 2002; Rosenbaum, 2005). Despite the cognitive revolution and the enthusiastic willingness to vanquish the S–R (stimulus–response) psychology of behaviourism, research on human action has continued to follow the classical behaviouristic methodology, although the paradigms have become increasingly sophisticated. The dominance of experiments based on stimulus-triggered responses is probably due to the fact that the researcher can easily quantify the subject's behaviour, for example, by measuring response times. By contrast, the quantification of actions that are triggered by some internal event is more difficult, as the researcher has no bearing on the timing and nature of decision processes involved in truly voluntary actions (i.e. the "what and when" of voluntary actions; Krieghoff et al., 2009).

Despite this major methodological obstacle, research on voluntary actions has witnessed a dramatic increase over the last one or two decades, to a large degree catalyzed by the advent of brain imaging techniques. Several recent reviews have covered functional, neuroanatomical, behavioural and psychophysiological aspects of this emerging domain (e.g., Haggard, 2008; Krieghoff et al., 2011; Nattkemper et al., 2010; Passingham et al., 2010; Shin et al., 2010). In contrast to these reviews, the current article revisits the literatures from different domains and integrates them from a particular theoretical perspective: manipulating one's surroundings to bring about desired effects presupposes internal representations of action-effect relationships. Without this knowledge goal-directed action would be impossible. Acquiring and using these representations for action preparation and evaluation is at the heart of voluntary action control. We will describe current knowledge of the role of action effect representations in voluntary action control, their neural basis and dynamics, as well as their functions. The aim of this review is to bring together current knowledge from research on action control and perception using psychophysical and imaging techniques to provide new insights into how the brain anticipates sensory action effects and how this anticipation influences the processing of the anticipated stimuli. Phenomena like sensory attenuation and intentional binding (defined later) will be subsumed under a common theoretical framework. This framework assumes that action preparation results in activation in perceptual areas representing the predicted sensory consequences of the action. This account explains sensory attenuation, for example, in that the activation due to the anticipation of the action effect constitutes an increased baseline from which the signal is less discriminable than from the baseline without effect anticipation. However, before bringing these elements together, we need to review several lines of research.

1. Ideomotor action

Only little is known about the functional properties of the voluntary action system. It has been suggested that voluntary actions are guided by the ideomotor and the common coding principles (cf., Lotze, 1852; Harleß, 1861; James, 1890; for a recent review see Shin et al., 2010). The ideomotor theory claims that performing an action results in a bidirectional association between the action's motor code and the sensory effects the action produces. Once acquired, these associations can be used to select an action by anticipating or internally activating their perceptual consequences (e.g., Greenwald, 1970; Prinz, 1997; Elsner and Hommel, 2001; Herwig et al., 2007). An illustrative example of an ideomotor action is that the idea to turn on the light activates the motor program necessary to press on the light switch. Related to the ideomotor approach of action control, and extending it, is the common coding theory. The common coding theory goes to such lengths as to claim that perception and action share a common representational code (e.g., Prinz, 1990; Hommel et al., 2001): actions are coded in terms of the distal perceptual effects they evoke in the environment. As a consequence, perceiving an action effect involves the same representation as performing the associated action and, conversely, performing an action involves the same representation as perceiving the associated effect.

The common coding principle has been corroborated by a number of studies. Hommel et al. (2001), Schütz-Bosbach and Prinz (2007) and Shin et al. (2010) review existing evidence in favour of the ideomotor theory of action control and the common coding approach in great detail. For example, Kunde (2001, 2003) showed that compatibility between responses and their sensory effects influences performance in choice reaction tasks. This indicates that the selection or execution of an action entails the internal anticipation of the sensory effect the system expects the given action to bring about the environment.

The anticipation of sensory effects as a principle of action control has also been embraced by computational models. In many models of action control a forward model does not only predict the future behavioural state of the system, but also the sensory consequences of that behaviour (Wolpert et al., 1995). Even more directly related to the ideomotor concept, many computational models include inverse models that provide the motor command which, given the particular current state, would result in a desired end state (e.g., a particular sensory effect; Wolpert et al., 1995).

Furthermore, action-outcome associations have also been widely investigated in animal learning experiments (see Balleine and O'Doherty, 2010 for a review). For example, findings from Pavlovian to instrumental transfer tasks (PIT; see Holmes et al., 2010), suggest that stimulus-reward associations can be transferred to action selection mechanisms through instrumental learning. For example, animals first learn associations between two different stimuli and two rewards (e.g., light flash and food or sound and sucrose). They are then rewarded for left and right lever presses with the same two rewards. In a subsequent test phase the animals will be more likely to select to press the lever previously associated with the relevant reward (e.g., food) upon presentation of one of the two stimuli (e.g., a light flash). Such findings point to the possibility that ideomotor theory is an extension of operant condition mechanisms that permeate much of human and animal behaviour. The aim of the present review is to integrate current knowledge on neurophysiological mechanisms of the anticipation of sensory action effects and to relate these mechanisms to perceptual phenomena like sensory attenuation, intentional binding and chromatic adaptation. However, one has to keep in mind that action effect anticipation is not an isolated function of the brain. It is only one particular aspect of action control and should ultimately be embedded into the broader context of behavioural control. In this context anticipated action outcomes serve as catalysts of action decisions and feedback functions teach the brain about the value of the given outcome, resulting in learning.

2. Neurophysiology of action outcome anticipation: MFC and cerebellum

Much effort has been dedicated to the identification of the neural substrate of voluntary action control. Recent fMRI studies show that the posterior medial frontal cortex (pMFC) is one of the key structures in this respect (see Fig. 1). The frontomedian wall comprises the supplementary motor area (SMA), subdivided into the



Fig. 1. Areas in the medial frontal cortex involved in effect anticipation. The figure shows the supplementary motor area (SMA) posteriorly to the supplementary eye field (SEF) and the pre-SMA. The SMA corresponds to mesial area $\delta a \alpha$, whereas the pre-SMA corresponds to mesial area $\delta a \alpha$, whereas the supel to differentiate pre-SMA from SMA activations. Ventral to this supplementary motor complex are the anterior and posterior rostral cingulate zones (RCZa and RCZp, often subsumed in under the terminology of the 'anterior cingulate cortex' (ACC)) and the caudal cingulate zone (CCZ).

Reprinted with permission from Nachev et al. (2008).

preSMA and the SMA proper, as well as the cingulate motor areas (CMA), subdivided into the rostral cingulate zone (RCZ), and the caudal cingulate zone (CCZ; Picard and Strick, 1996). The posterior medial frontal cortex has been suggested to be involved in various functions related to action control, such as internal selection and timing of action (Krieghoff et al., 2009; Cunnington et al., 2002; Cunnington et al., 2002, 2005; Mueller et al., 2007), resolution of conflict between different condition–action associations (Nachev et al., 2008), conflict monitoring (Kerns et al., 2004; Botvinick et al., 2001; Carter et al., 1998; Liston et al., 2006), error processing (Debener et al., 2005; Menon et al., 2001; Swick and Turken, 2002), and task-set related control (Brass and von Cramon, 2002; Rushworth et al., 2002; Crone et al., 2006).

We do not want to review the literature on the neurophysiological substrate of voluntary action control extensively. For reviews in this context see Haggard (2008), Krieghoff et al. (2011), Rushworth et al. (2004, 2007) and Picard and Strick (1996). Instead, we would like to focus on studies, which suggest that the pMFC is also involved in relating actions to their consequences and is, thus, an essential area for ideomotor action. Evidence comes from both studies on monkeys and on humans. However, while studies on monkeys focus rather on action outcomes that are either positive or negative reinforcement, studies on humans concern rather sensory action outcomes that do not have an intrinsic value.

In the light of several non-human primate studies investigating reward-guided action control, Rushworth et al. (2007) conclude that the ACC plays a major role in making decisions based on the history of previous actions and their consequences. In this view, ACC represents the relationship between a particular action and its outcome in terms of its reinforcement value. For example, Matsumoto et al. (2003) recorded from neurons in the MFC (they do not further specify from which region in particular they recorded) while monkeys performed a go/no-go task in response to one of two visual cues. Importantly, Matsumoto and colleagues varied the relationships between the cues, the response in the go/no-go task and the reward independently, allowing them to observe MFC neurons in all eight possible cue - response - reward combinations. They found that, even before the response, many neurons discharged as a function of the expectation of reward or non-reward (25%), the intention to respond or not (25%), or a

combination of intention and expectation (11%). Another example is the study of Amiez et al. (2006) showing by means of single cell recordings that when macaques have to choose between two actions that are probabilistically associated with rewards of different value (e.g., 1.2 ml of juice with a probability of 0.7 and 0.4 ml of juice with a probability of 0.3 [average reward over trials = 0.96 ml] vs. 1.2 ml with a probability of 0.3 and 0.4 ml with a probability of 0.7 [average reward over trials = 0.64 ml]), activity of many ACC neurons represent the mean value of the reinforcement history of the action. This activity in ACC was observed even prior to discovery of the optimal stimulus (yielding the higher reward across trials) suggesting that ACC plays a role in guiding voluntary behaviour dependent on reward outcomes: a conclusion further confirmed by the observation that muscimol deactivation of the ACC resulted in an impairment in finding the optimal stimulus.

Lesion studies point towards a similar conclusion. Lesions in the prelimbic cortex of rats results in behaviour being no longer driven by outcomes, but only by habit (Balleine and Dickinson, 1998; Killcross and Coutureau, 2003). In their review of these and other studies, Rushworth et al. (2004, 2007) conclude that the ACC is involved in representing action-outcome relationships and conceiving possible beneficial consequences of a given option for action. It is important to note that ACC has also previously been associated with conflict monitoring (Botvinick et al., 2001) processes. However, one way to reconcile these accounts is to view ACC as a region involved in optimizing behaviour and action selection. In this way it seems plausible that both past experience (reinforcement history) and current task demands (task difficulty and arousal) should be taken in to account to ensure effective behavioural control (for a comprehensive review of this issue see Botvinick, 2007).

Research on humans corroborates the notion that the MFC is involved in the anticipation of action outcomes. However, this research stresses the role of other areas within the MFC. Haggard and Whitford (2004) investigated the neurophysiological underpinnings of sensory attenuation. Sensory attenuation refers to the phenomenon that self-produced sensations are perceived attenuated compared to identical but externally produced stimuli. Haggard and Whitford studied the perceived size of TMS-evoked (transcranial magnetic stimulation) finger-muscle twitches. Participants freely chose on each trial whether or not to make a finger flexion in synchrony with a cue. They showed that muscle twitches evoked by TMS over the primary motor cortex (M1) were perceived to be smaller when participants made intention-based actions than when they did not, demonstrating sensory attenuation. Moreover, Haggard and Whitford showed that a conditioning TMS prepulse transiently disrupting the supplementary motor area (SMA) before the test pulse producing the muscle twitch almost abolished the sensory attenuation effect. They concluded that the SMA sends an efferent signal of anticipated sensory effects to posterior brain areas to attenuate somatosensory activity during intention-based action. Sensory attenuation will be discussed in more detail below. Suffice it to mention at this point that, at the end of this review, we will discuss an account of this phenomenon that resolves the apparent incompatibility between the notion that action and effect share a representation (ideomotor theory) and the notion that motor preparation attenuates or suppresses representations.

The findings of Haggard and Whitford (2004) are in agreement with a study from Voss et al. (2006). These authors measured sensory attenuation of briefly applied electrical cutaneous stimuli using TMS over M1 to delay motor commands during voluntary action. Even during this delay, that is, prior to the onset of the movement, Voss et al. observed sensory attenuation. This suggests that sensory attenuation is related to movement preparation (rather than its execution) and takes place upstream of primary motor cortex. Moreover, studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) demonstrated the SMA to be a central structure for the representation of newly learned action–effect associations (Elsner et al., 2002; Melcher et al., 2008; see also Ticini et al., in press). Elsner et al., for example, made participants learn that voluntary key presses were consistently followed by certain tones. Using PET imaging, they showed that passively listening to these action–effect tones resulted in increased activity in the caudal supplementary motor area (and the right hippocampus). Although this study does not show that effect anticipation is functional in action selection, it demonstrates that voluntary action results in the compilation of action–effect associations and that the SMA is a crucial area in linking actions and their effects.

However, the SMA complex is not the only structure in the human MFC that has been involved in action effect prediction. Recently, Hughes and Waszak (2011) used a paradigm in which voluntary actions were either associated with a visual action effect or to no effect. They studied both sensory attenuation (by comparing event-related potentials (ERPs) to action-triggered vs. externally triggered stimuli) and, more importantly in the present context, action effect prediction (by comparing ERPs of actions that triggered a stimulus with actions that did not). Participants were required to choose on each trial whether to perform an action with their left or right hand, with only one of the two actions resulting in a visual action effect (counterbalanced across participants). Rather than observing differences in the readiness potential (RP; a slow negative deflection in the EEG thought to reflect unspecific motor preparation in SMA), Hughes and Waszak observed a significantly increased lateralized readiness potential (LRP) for action-to-effect trials compared to action-only trials. The LRP is thought to reflect lateralized (i.e. action-specific) activation in M1 (see Coles, 1989; Leuthold and Jentzsch, 2002), suggesting that, in the experiment from Hughes and Waszak, M1 and not SMA may have been involved in the prediction of a visual action-effect.

The same conclusions can be drawn from the study of Voss et al. (2007). These authors investigated a phenomenon previously demonstrated by Shergill et al. (2003), namely that participants consistently overestimate the force required to reproduce tactile stimulation applied to their finger, an effect considered to be based on effect anticipation (see below). Voss et al. showed this effect to be reduced following theta burst stimulation of primary motor cortex.

In summary, monkey and human research have gathered evidence indicating that the motor system, notably the posterior MFC and M1, has a vital role in representing and predicting the outcome of actions. Although not in the focus of the present review, it might be revealing that (monkey) studies dealing with action outcomes that are intrinsically rewarding consistently point to a crucial role of the ACC, whereas research (on humans) studying sensory action effects suggest an important role for the adjacent SMA (and maybe M1). This could be taken to indicate that SMA is related to the anticipation of the sensory consequences of an action, whereas ACC is involved in the anticipation of the reinforcing value of the action. However, notice that, to the best of our knowledge, mechanisms of sensory and reward anticipation have not yet been directly compared to each other. The notion of a putative neurofunctional dissociation within the pMFC, thus, needs to be taken with caution.

In addition to cortical motor areas, the cerebellum has been implicated in predictive action mechanisms. For example, Morton and Bastian (2006) showed, using a special splitbelt treadmill allowing independent control of the speed of left and right side of the treadmill that while patients with cerebellar lesions are able to make reactive adaptations to sudden changes in the speed of one of the belts, they were unable to take into account the asynchronous movements to more efficiently plan subsequent steps. Bastian (2006) suggests that the cerebellum generates an internal predictive model of sensory states that can be used to learn sensorimotor associations to facilitate feedforward motor control.

A number of studies by Blakemore et al. (1998, 1999b, 2001) suggest that the cerebellum might be similarly involved in the types of sensorimotor contingencies involved in sensory attenuation and intentional binding. For example, Blakemore et al. (1998) showed that brain activity (as measured by fMRI) was reduced in somatosensory cortex for self-tactile stimulation compared to the externally triggered stimulation - evidence of sensory attenuation (see below). They also found that right anterior cerebellar cortex showed decreased activity for actions that resulted in tactile stimulation but not for movement alone, while activity was significantly increased for externally produced tactile stimuli. The cerebellum, thus, differentiates between movements with different sensory consequences. In a further study (Blakemore et al., 1999b) they showed using a psychophysiological interaction (PPI) analysis that the degree of modulation in the cerebellum was correlated with activity in thalamus and somatosensory cortex, suggesting that predictive activity in the cerebellum contributes to the reduced activation in somatosensory cortex and sensory attenuation. Furthermore, they observed that activity in the cerebellum was positively correlated with the degree to which the tactile stimulation was delayed relative to the participants' own movements (Blakemore et al., 2001), suggesting that the cerebellum signals the magnitude of the discrepancy between the predicted and observed consequences of one's movements. An interesting question is the degree to which cerebellum activity might correlate with sensory attenuation in a task where rather than making fine movements with one hand participants' are required to make a simple button press (e.g., Baess et al., 2008, 2009; Hughes and Waszak, 2011). Given the role of cerebellum in motor co-ordination described above, the cerebellum might be more involved in prediction processes that concern fine motor commands, such as the discordance observed when tickling oneself, but not when participants are simply required to press a button to produce a desired goal. In this way cerebellum and SMA may have complementary roles, with the former involved in predictions regarding fine motor co-ordination and the later in higher-level decision-making.

3. Neurophysiology of action outcome anticipation: perceptual areas

An evident question in the context of the neurophysiological basis of action effect anticipation is whether the action–effectrelated activity in the MFC (and cerebellum) goes along with a corresponding activity in perceptual areas. This is what would to be expected from an ideomotor theory/common coding viewpoint, since performing an action should involve the same representation as perceiving the effect it is associated to.

Kühn et al. (2010) tested this notion using fMRI. They measured action-induced activity in areas that are known to be involved in the perception of particular classes of stimuli, harrnessing the modularity of perceptual category representation in the human brain. In particular, it has been shown that faces and houses are represented in the fusiform face area (FFA; Kanwisher et al., 1997) and in the parahippocampal place area (PPA; Epstein and Kanwisher, 1998), respectively. Kühn and colleagues made subjects acquire an association between left and right key presses and face and house stimuli, respectively, as action effects. They were able to test subsequently whether performing an action in the absence of face and house effect stimuli yields activity in cortical areas involved in the perceptual representation of the sensory effects which the actions used to trigger. Contrary to other experiments used in this context



Fig. 2. Illustration of the results from Kühn et al. (2010). In this experiment, using fMRI, participants had first to respond at random either with the left or the right hand when a white square appeared on the screen (baseline phase). In the subsequent acquisition phase, the same right and left hand actions were consistently followed by a certain stimulus category (e.g., right \rightarrow face, left \rightarrow house). The test phase of the experiment was identical to the baseline phase. The figure shows percent signal changes between baseline and test phase of ROIs in (A) bilateral fusiform face area (FFA) and (B) bilateral parahippocampal place area (PPA), separately for the two actions. Reprinted with permission from Kühn et al. (2010).

(e.g., Elsner et al., 2002), this design has the essential advantage that neural consequences of action effect anticipation can be assessed without presenting the effects as stimuli.

During the baseline phase, i.e., before the associations were acquired, activity in FFA and PPA did not depend on which action was performed. However, activity in the test phase was elevated in the FFA for actions that in the acquisition phase triggered presentation of face stimuli (compared to actions that previously triggered house stimuli). The opposite was true for the PPA (see Fig. 2). These differences in activity were observed in the absence of any visual stimulation. It is thus the action itself that induces activation in FFA and PPA, corroborating the ideomotor principle of action control and the common coding principle. This study suggests that the activation of the perceptual representation of the action's sensory effects becomes an integral part of the action itself (for a similar result see Kühn et al., 2011). This finding also provides evidence that the type of effects previously observed (e.g., Elsner et al., 2002, see above) likely results from activation of brain areas associated with the learnt action-effect when performing the action.

Notice that FFA and PPA are areas that have been tightly linked to the perception of faces and houses, respectively. This is nicely demonstrated by experiments using binocular rivalry. For example, Tong et al. (1998) presented face and house stimuli to different eyes of the participants. During this binocular rivalry participants experience a bi-stable percept of alternating faces and houses. Tong et al. showed that these alternations in perception were tracked by changes in PPA and FFA activity. The results from Kühn et al. (2010) summarized above thus indicate that performing an action entails activity in, at least certain, perceptual areas as if the stimulus that the action previously triggered is actually perceived.

Action-induced activity in sensory areas has also been demonstrated in the auditory domain. In an acquisition phase, Kühn and Brass (2010) made participants decide between performing an action and not performing it. Both these decisions triggered presentation of a tone. In a subsequent test phase participants carried out (or did not carry out) actions without hearing the effect tone. Actions (and also non-actions) that previously triggered a tone yielded increased activity in the auditory cortex. (The fact that also non-actions triggered activity in auditory cortex might indicate that to "perform a non-action" involves a motor decision and possibly also motor preparation (of a finally not-executed action), just as performing a real action does.)

However, there is still relatively little data concerning actioncontingent activations in perceptual areas. It is unclear how general this phenomenon is and on which levels of representation it occurs. FFA and PPA, for example, located in the temporal lobe, are associated to higher-order visual processing. But we do not know whether there are also action-contingent activations in areas in charge of earlier processing stages in extrastriate or even striate cortex.

Another unanswered question concerns the dynamics of these activations, i.e., whether they are related to preparatory stages of motor processing or rather to the execution of the action. The question is of importance since it differentiates between a strong and a weak version of the ideomotor theory (cf. Ziessler and Nattkemper, 2011). A strong version assumes that effect anticipation is an integral part of action selection (e.g., James, 1890; Prinz, 1997). Effect anticipation should therefore take place at early stages of motor preparation. A weak version posits that effect anticipation is rather used for quality control and error handling. In this view, effect anticipation could occur at later stages of motor preparation.

4. Processing of action effects

Up to now we have discussed current knowledge about mechanisms of action effect anticipation. However, in most models of voluntary motor control, action consequences are not only anticipated but they are also compared to the actual sensory consequences of the action. In this "closed-loop control" system it is not only that the process input (motor command) has an effect on the process output (action effect), but also that the latter is fed back to the controller and compared with the desired (anticipated) output (e.g., Frith et al., 2000). The result of this comparison can be used to optimize behaviour.

Different paradigms have been used to study processing of anticipated and not anticipated action effects, providing evidence regarding different aspects of voluntary action control including attentional processes, learning, agency and perception of action effects. Broadly speaking, the paradigms can be divided into two classes: those focusing on the consequences of a match between anticipated and actual effect and those focusing on the consequences of a mismatch.

4.1. Processing of unanticipated action effects

Anticipating the sensory consequences of our actions helps us to optimize the accuracy and speed of complex action sequences, where actions often depend on the outcome of the preceding action. However, the effect of an action is not always borne out as expected. Unanticipated effects should elicit processes of error-handling that makes the given event available to behavioural control. One class of paradigms widely used to study brain mechanisms dedicated to monitoring performance assesses the Error-Related Negativity (ERN; e.g., Falkenstein et al., 1990). The ERN is a negative deflection occurring when humans commit errors in reaction-time tasks or when they receive negative feedback about their performance (feedback-related negativity [N_{FB}]; Miltner et al., 1997). Converging evidence indicates that the ERN is generated in the anterior cingulate cortex (ACC; e.g., Dehaene et al., 1994). Holroyd and Coles (2002) argued that the ERN reflects the transmission of the reinforcement signal from the mesencephalic dopamine system to the ACC. Errors or negative feedback induce phasic decreases in mesencephalic dopamine, whereas correct responses induce phasic increases. The ACC harnesses this signal to reinforce successful motor routines. The ERN, so the reasoning goes, is generated on error trials, but not on correct trials, when the reduction of dopaminergic input disinhibits certain neurons in the anterior cingulate cortex.

Band et al. (2009) devised a probabilistic learning task allowing for the comparison of the processing of explicit, performance related feedback with the processing of learned task-irrelevant response-contingent action effects. They replicated findings showing that negative performance feedback produces a feedbackrelated negativity (N_{FB}). Importantly, Band et al. demonstrated that unexpected but task-irrelevant action effects elicit a signal similar to the N_{FB} (see Fig. 3). They referred to this signal as action–effect negativity (N_{AE}). This finding suggests once more that acquired action–effect associations give rise to the anticipation of the perceptual consequences of a given action. To be precise, it shows that a mismatch between anticipated and actual action effect results in an N_{AE}, which, analogous to the N_{FB}, probably reflects processes related to outcome evaluation and associative learning.



Fig. 3. Results from Band et al. (2009). Average ERPs time-locked to the auditory stimulus triggered by the participants' action. The auditory stimulus was either relevant positive or negative feedback (left panel) or it was an irrelevant high or low probability action effect (right panel). Left panel: The comparison of positive and negative feedback reveals typical feedback negativity and positivity (N_{FB} and P_{FB}). Right panel: The comparison of high-probability (80%) and low-probability (20%) action effects reveals an effect-related negativity (N_{FB}) similar to the N_{FB}. Reprinted with permission from Band et al. (2009).

Similarly, Waszak and Herwig (2007) showed that orienting responses to a deviant stimulus can be modulated by manipulating anticipatory motor processes. Based on a series of experiments from Nittono and colleagues (Nittono, 2006; Nittono and Ullsperger, 2000; Nittono et al., 2003), Waszak and Herwig used a three-tone oddball paradigm to address this question. The experiment had an acquisition phase and a test phase. In the acquisition phase participants performed self-selected key presses that triggered contingently a certain tone (e.g., left key press \rightarrow high pitch tone [1940 Hz, later used as the standard stimulus]; right key press \rightarrow low pitch tone [500 Hz, later used as the deviant stimulus]), thus establishing an association between actions and corresponding effect tones (cf., Elsner and Hommel, 2001). In the test phase, participants performed an oddball task. They were presented with either a high-probability stimulus, the target, or a low-probability stimulus, the deviant. Importantly, stimulus presentation in the test phase was triggered by the participants' voluntary key presses. As in the learning phase, participants were required to choose between left and right key presses which triggered randomly the standard or the deviant stimulus, with a high and a low probability, respectively.

Since, depending on the action performed on a given trial, the participants anticipated either the standard or the deviant stimulus (due to the link established in the acquisition phase), the participants' anticipation was or was not fulfilled. Waszak and Herwig (2007) found that deviant tones elicited a smaller P3a when the action that triggered stimulus presentation anticipated the deviant tone than when it anticipated the standard tone. A vast literature on electrophysiological correlates of the processing of deviant auditory events (see, for example, Näätänen, 1990; Friedman et al., 2001) has shown that the P3a, an eventrelated potential (ERP) occurring about 300 ms post-stimulus with a fronto-central topography, reflects a frontal lobe function related to orienting of attention (see Posner and Petersen, 1990). The finding from Waszak and Herwig, thus, demonstrates that the internal anticipation of an action's effect modulates the orienting response to deviant stimuli.

Taken together, these results suggest that humans monitor the sensory input for action effects that do not meet their anticipations. Unanticipated action effects seem to be treated as a critical problem of the ongoing agent–environment interaction that indicates the need for immediate action correction and interruption of learning.

4.2. Processing of anticipated action effects: sensory attenuation

The last decade has witnessed a large number of studies showing that action effects are processed differently when compared to stimuli that are externally triggered. Notably, it has been shown that voluntary actions result in attenuation of the action's sensory effect (e.g., Blakemore et al., 1998). The most well known example of sensory attenuation is that it is difficult to tickle oneself. Blakemore et al. (1999a) investigated this phenomenon experimentally. They made participants tickle their right palm by means of a robotic arm controlled with their left hand. They found that introducing a spatial or temporal perturbation to participants' self-stimulation lead to an increase in the perceived ticklishness, suggesting that more accurate prediction results in greater attenuation (Blakemore et al., 1999a). Similarly, Shergill et al. (2003) showed that participants consistently overestimated the force required to reproduce tactile stimulation applied to their finger. Using a similar methodology, Bays et al. (2005) showed that selfstimulation of the left-hand with the right-hand (by tapping on a sensor placed above the left hand which was in turn connected to a motor to directly stimulate the left hand) resulted in reduced sensation of the tap on the left hand, compared to a tap in the absence of any movement. Attenuation was reduced when the tap did not occur in synchrony with the action, and was abolished if participants aborted their left-hand action prior to reaching the sensor or if they tapped next to the sensor. Bays et al. (2006) further showed that if the sensor was unexpectedly moved prior to their finger making contact, sensory attenuation was still present. This suggests that prediction of the action–effect along with commencement of the action itself was sufficient to produce sensory attenuation, even if the action was not successfully completed.

In addition to these results in the somatosensory domain, sensory attenuation has been observed for both auditory (Sato, 2008) and visual action effects (Cardoso-Leite et al., 2010). Cardoso-Leite et al., for example, assessed the influence of the congruency between anticipated and actual action effect on the detection of the latter. For almost all subjects, detection performance in the congruent condition was worse than in the neutral and incongruent conditions, demonstrating sensory attenuation.

Sensory attenuation has not only been studied as a perceptual phenomenon, but also, using imaging techniques, as a neurophysiological effect. Differences in cortical responses between self-produced and externally presented stimuli have been found to be similar to the difference in phenomenology (e.g., Aliu et al., 2009; Baess et al., 2008; Blakemore et al., 1998, 2000; Hughes and Waszak, 2011; Schäfer and Marcus, 1973). Using fMRI Blakemore et al. (1998) showed that activity in somatosensory cortex was greater when a piece of foam used to tickle participants' left hand was controlled by the experimenter compared to when it was moved by their own right hand. Similarly, self and externally triggered stimuli have been compared by means of ERPs (Schäfer and Marcus, 1973; Aliu et al., 2009; Baess et al., 2008, 2009; Hughes and Waszak, 2011). For example, Baess et al. (2008) found a reduced auditory N1 component for action-triggered tones compared to externally triggered tones, suggesting that cortical activity was attenuated for the former. Baess et al. (2009) demonstrated the same attenuation for middle latency auditory responses and 40 Hz responses, supposed to reflect early brain activity in response to sound events in subcortical and auditory cortical areas, suggesting that cortical sensory attenuation occurs at a relatively early stage of sensory processing. Hughes and Waszak (2011) compared ERPs to action-triggered vs. externally triggered stimuli and found attenuated cortical responses elicited by visual effects in a frontoparietal network, starting 150 ms after stimulus.

Both attenuated *phenomenological* and *neurophysiological* responses are usually interpreted along the lines of forward models discussed above (e.g., Miall and Wolpert, 1996): The motor system produces an "efference copy" of the motor command (e.g., Von Holst and Mittelstaedt, 1950), which is used to predict the sensory consequences of the given action (the corollary discharge). The corollary discharge is compared with the true sensory feedback. If predicted and true action effect match, then the representation of the action effect is attenuated.

We would like to point out two caveats in this context. First, almost all studies on phenomenological sensory attenuation used the point of subjective equality or other classical psychophysical techniques (e.g., Haggard and Whitford, 2004; Sato, 2008). According to signal detection theory (Green and Swets, 1966) a sensory process transforms the stimulus energy into an internal response (or representation) and a decision process decides on each trial whether or not to consider the stimulus to be present based on the current value of the internal response and the decision criterion. The difference in the shape (i.e., mean and standard deviation) of the distributions of internal responses elicited in trials in which the stimulus is physically present ("signal" distribution) vs. in which the stimulus is physically absent ("noise" distribution) characterizes sensitivity (d'). The higher d' (i.e., the further apart the two distributions are), the better the perceptual system is able to differentiate signal from noise. The decision or response criterion (c) is the value that the internal response has to exceed in order for the participant to report the stimulus to be present. The lower c, the smaller are the internal responses that the perceptual system still accepts as "stimulus present". Importantly, sensitivity and response criterion, both of which affect the percentage of correct responses, are confounded by the methods usually used to investigate the phenomenology of sensory attenuation. As a consequence, they cannot rule out that the sensorimotor contingencies alter simply the participants' response bias rather than the perception of the action consequence.

To our knowledge only a single study tested whether internal action-effect anticipation genuinely alters the perception of the effect or whether it merely induces a response bias: the experiment by Cardoso-Leite et al. (2010) compared participants' detection performance to stimuli (tilted Gabor patches presented at detection threshold) in three different conditions: the stimuli were triggered by an action involving the internal anticipation of a learned visual effect, that is, either (1) congruent or (2) incongruent to the to-bedetected threshold stimulus, or (3) neutral. Using signal detection methodology they were able to assess the influence of the congruency between anticipated and actual action effect on the detection of the latter, separately for d' and c. Cardoso-Leite et al. found d' in the congruent condition to be smaller than in the neutral and incongruent conditions (see Fig. 4). At the same time c was identical for the three conditions. The results, thus, suggest that internal action-effect anticipation truly affects perception (at least in the visual domain). However, given how crucial this is for any forward model interpretation of sensory attenuation, there is an astonishing paucity of data concerning this issue.

The second caveat concerns the fact that, to the best of our knowledge, no study assessed both neurophysiological indices and perceptual indices of sensory attenuation at the same time. It is, therefore, difficult to relate the attenuation of perceptual awareness to the attenuation of cortical responses that have been observed time and again in separate experiments. This issue is of importance since differences of cortical responses between the conditions with and without effect anticipation can very often not be unambiguously attributed to differences in sensory processing, but may also be caused by other differences in attentional and cognitive processing. Consequently, results from different studies do not always converge to the same conclusions. Just to give an example, Baess et al. (2008) interpreted the attenuated frontocentral negative component they observed when comparing action-triggered vs. externally triggered auditory stimuli in terms of reduced early sensory processing in the auditory cortex. However, using visual stimuli Hughes and Waszak (2011) found a significantly increased visual P1 component for anticipated effects and not a decreased P1 as one would expect if processing in primary sensory cortex was attenuated. Instead, they report evidence for reduced later processing of the stimulus, reflected in a reduced frontocentral negativity from around 150 ms after stimulus onset in the action-to-effect condition, followed by a reduction in the parietal P3 component. They consider this result to be in line with recent findings showing that subjective thresholds of visual stimuli is reflected in later processing in a frontoparietal network, rather than in early visual areas (Del Cul et al., 2007). However, without concurrent assessment of perceptual indices of sensory attenuation, neither early nor late components can be unequivocally related to the reduced awareness of the action effects.

Hughes and Waszak (2011) also noted that the reduced frontocentral negativities of their own study and the study of Baess et al. (2008) bear resemblance in latency and topography to a typical N2 component, which is considered to be generated in anterior cingulate cortex (Debener et al., 2005). As mentioned above, Holroyd and Coles (2002) believe this component to reflect the transmission of a negative reinforcement signal from the mesencephalic dopamine



Fig. 4. Results from Cardoso-Leite et al. (2010). In the acquisition phase of this experiment left- and right-key presses were associated with Gabor patches of +45° or -45° of orientation, respectively. In the test phase, participants' key presses triggered the onset of a low-contrast Gabor patch on 50% of trials; no Gabor patch was displayed on the remaining 50%. The Gabor patch was either the same (e.g., 45°; congruent), the alternative (e.g., -45°; incongruent), or a Gabor patch not used in the acquisition phase (0°; neutral). For details of the design see Cardoso-Leite et al. Participants were asked to report whether or not they had seen a Gabor patch. The figure shows the effect of the acquired action-effect association on visual sensitivity (d'; top panel) and the decision criterion (c; bottom panel) in the test phase. The difference in d'/c between the congruent and neutral Conditions. The figure shows that compared to incongruent and neutral Gabor patches congruent Gabor patches show a reduced sensitivity (d'). The criterion c, by contrast, does not differ between conditions.

Reprinted with permission from Cardoso-Leite et al. (2010).

system to the ACC and Band et al. (2009) showed that a similar component was enhanced following unanticipated action effects. As a consequence, it is possible that attenuated frontocentral components in the time range of an N2 reflect the reduced need to engage these cognitive control mechanisms instead of reduced activity in auditory cortex as assumed by Baess et al. (2008). This interpretation is similar to that offered by Schäfer and Marcus (1973), who suggest that their effects recorded over the vertex for visual and auditory stimuli reflect a non-domain-specific mechanism of attenuation. Although there is evidence suggesting that auditory cortex activity is indeed attenuated to auditory action effects (reduced mid-latency ERP response [Baess et al., 2009] and source localized MEG responses [Aliu et al., 2009]), future research should include both objective and subjective measures of sensory attenuation. Only then we will be able to understand which of the diverse components that have been associated with sensory attenuation truly reflect attenuated perceptual awareness, which are due to other factors and whether differences between sensory domains exist.

Taken together these findings suggest that sensory attenuation is likely reflected in modulation of both sensory ERP components (particularly for auditory stimuli) and later components associated with a reduced engagement of cognitive control processes in response to an expected sensory event. This latter modulation could thus be seen as neural processing associated with expectedness, such that it is attenuated for predicted stimuli but also increased for unexpected stimuli (as described in the previous section). In contrast, any early modulation of sensory components might be reduced only when the specific sensory event is predicted, but not increased for deviant or unexpected stimuli, as compared to other unpredicted stimuli. In this way the neural indices of sensory attenuation, and cognitive control processes remain partially dissociable.

4.3. Processing of anticipated action effects: chromatic judgments

Only very rarely discussed in the context of action effect anticipation are a number of studies that assessed chromatic adaptation due to eye movements associated with particular chromatic changes in perception (Bompas and O'Regan, 2006a,b; Richters and Eskew, 2009). Richters and Eskew, for example, made subjects perform for about 40 min leftward eye movements towards a red stimulus, and rightward eye movements towards a green stimulus. Before and after this training, participants' color judgments were assessed by asking them to compare the color of two stimuli after leftward and rightward saccades respectively. They report that the point of subjective equality (PSE) shifted as a result of the learning phase: stimuli looked redder after a rightward saccade and greener after a leftward saccade. In several control experiments Bompas and O'Regan (2006a, 2006b) and Richters and Eskew (2009) showed that this is truly a sensorimotor effect (e.g., associating the color change to a tone did not produce the same effect [Richters and Eskew, 2009)]). 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 a green stimulus, demonstrating that the mechanism producing the effect is of a general nature and not restricted to eye movements.

Note that PSEs were shifted as if the participants perceived the stimuli in a hue opposite to the hue that was associated with the eye/joystick movement in the learning phase. The movements did not simply evoke the associated color. Instead, the effect was in the same compensatory direction as in experiments on chromatic adaptation, where the, say, "redness" of a stimulus diminishes with exposure to a red stimulus (see Jameson and Hurvich, 1972). Hence, just as performing an action associated with a particular Gabor patch reduces the agent's sensitivity to that Gabor patch (Cardoso-Leite et al., 2010), performing an action associated with a particular color change results in a reduced sensitivity for the associated color. We will return to this issue later.

4.4. Processing of anticipated action effects: intentional binding

Another phenomenological consequence of action effect anticipation that has been widely investigated in the last decade is the sense of agency and, as an implicit measure of it, intentional binding (e.g., Haggard et al., 2002; Moore and Haggard, 2008). The sense of agency refers to the fact that people are easily able to distinguish self-produced action effects and action effects produced by others. It is the experience of being the cause of a sensory event. The intentional binding effect, see Fig. 5, refers to the fact that when a voluntary movement is followed by a sensory effect, the awareness of the voluntary movement is shifted towards the subsequent sensory effect, whereas the awareness of the effect is shifted towards the movement (compared to a movement only/effect only condition; e.g., Haggard et al., 2002). Researchers have frequently used this intentional binding effect as an implicit measure of the sense of agency, because it has been found that intentional binding occurs reliably in situations in which the participant performs a voluntary action whereas it does not occur with involuntary movements induced by transcranial magnetic stimulation (TMS) or with passive movements (Engbert et al., 2008; Haggard and Clark, 2003; Haggard et al., 2002).

The most commonly used paradigm to assess intentional binding is the rotating clock-hand procedure (e.g., Desantis et al., 2011; Haggard et al., 2002; Haggard and Clark, 2003; Haggard and Cole, 2007; Moore and Haggard, 2008) that was originally conceived by Libet et al. (1983). In this paradigm participants are presented with a clock face marked with 5 min intervals and a clock hand that typically rotates with a period of 2560 ms (Libet et al., 1983; Haggard et al., 2002). Participants are required to report the position of the clock hand at the time when the event to be judged in the particular trial occurred (usually the onset time of an external stimulus or the time of a voluntary action). However, since the Libet method has been subject to substantial criticism (e.g., Gomes, 2002), some recent studies have assessed numerical judgments of the time interval between action and effect (e.g., Engbert et al., 2007, 2008), or employed a time interval replication task (by holding down a response button to replicate the perceived time; Humphreys and Buehner, 2009; Buehner and Humphreys, 2010). Other studies have used a synchrony judgment task (Cravo et al., 2011) or asked participants to make a button press in synchrony with the action-effect (Buehner and Humphreys, 2009). These studies provide validation of the phenomena of intentional binding using a number of different experimental paradigms, all converging on the same result, namely that action effects are bound in time towards the action that causes them.

It has been suggested that both the sense of agency as well as the capacity to distinguish externally and self-produced effects arise from internal movement generation (Blakemore et al., 2002; Frith, 2005; Sato and Yasuda, 2005). Just as outlined above in the context of sensory suppression, a forward model is thought to anticipate the sensory effect of a given action (cf. Wolpert, 1997). If predicted and actual sensory effects match, the sensory action consequence is considered to be self-generated and the agent experiences the feeling of agency. If they do not match, then the sensory effect is considered to be an external event. An alternative approach claims that the sense of agency depends rather on postdictive interpretative processes than on predictive sensorimotor processes (Wegner, 2003). According to this account it is a match between prior conscious thoughts and the observed outcome of the action that makes the agent infer retrospectively that he or she was at the origin of the sensory event. More recently, it has been noted that these two accounts are not mutually exclusive, but that both sensorimotor and interpretative processes may contribute to the sense of agency (Bayne and Pacherie, 2007; Synofzik et al., 2008; Pacherie, 2008; Moore and Haggard, 2008; Moore et al., 2009a,b). However, a comprehensive review of different accounts of the sense of agency is beyond the scope of the present article.

More recently, it has also been investigated whether contextual beliefs (to be the cause of an effect) modulate low-level sensorimotor processes. Desantis et al. (2011), for example, tested whether causal beliefs influence intentional binding. In their experiment participants judged onset times of actions and of sounds triggered by the action. Desantis and colleagues made subjects believe that the tone was either triggered by themselves or by



Fig. 5. Example of the intentional binding experiment of Moore et al. (2010) (Figs. 1a and 2a). Participants watched a clock face revolve at one revolution every 2560 ms and were required to perform a right hand voluntary key press action at the time of their choosing (a). This key press triggered a mild electric shock to the right little finger after an interval of 250 ms. Participants were asked to report, in a baseline condition containing only voluntary actions or shocks, the perceived time of these events. They reported this time by noting the position of the clock hand at the time when the action or shock occurred. In the experimental conditions all trials included both a voluntary action and a shock, with participants always being asked to rate the timing of one of the two events. Moore et al. (2010) used theta-burst stimulation (TBS) to disrupt activity in the pre-SMA or contralateral sensorimotor hand area to assess the influence of these brain regions in intentional binding. They compared the results from these sessions to TBS over sensory leg areas, which acted as a control condition. They observed binding in all 3 TBS conditions as shown by the positive shift in the perceived time of the effect, compared to the baseline (b). Additionally, the perceived negative shift in time of the shock was significantly reduced following pre-SMA stimulation compared to the control condition, confirming the role of pre-SMA in intentional binding. Reprinted with permission from Moore et al. (2010).

somebody else, although, in reality, it was always triggered by the participants. They found intentional binding to be stronger when participants believed that they triggered the tone, compared to when they believed that another person triggered the tone. These results suggest that high-level contextual information influences sensorimotor processes responsible for generating intentional binding.

5. Anticipation, control, temporal prediction

Both intentional binding and sensory suppression have been linked to internal forward models that predict the sensory consequences of motor commands in advance of the true sensory feedback. However, the precise nature of the predictive mechanisms involved are still to be clarified. In particular, an explanation in terms of action effect prediction assumes that the internal anticipation is 'effect specific', i.e., it is a particular sensory effect that is predicted (and then bound/attenuated). As outlined in previous sections, there is overwhelming evidence that effect specific prediction does occur, with a number of behavioural (e.g., Kunde, 2001) as well as neuroimaging studies (e.g., Elsner et al., 2002; Kühn et al., 2010) showing that different actions show learnt associations with different sensory events. However, many contrasts used to explore sensory attenuation and intentional binding differ in terms of a number of factors. It is, thus, unclear, whether these phenomenological consequences of voluntary action are based on effect specific prediction rather than being general consequences of motor actions. In this section we will describe the possible role of temporal prediction, temporal control and different identity prediction mechanisms in previous published reports of sensory attenuation and intentional binding.

Schäfer and Marcus (1973) tested sensory attenuation by comparing visual and auditory stimuli that were triggered by voluntary actions with stimuli triggered by a machine. In addition to the presence of an action in only one of these conditions, they also differ with regards to the temporal predictability of the stimuli, such that in the action condition their onset is completely predictable, while in the other condition their onset is unpredictable. Schäfer and Marcus (1973) included an additional condition to control for temporal expectancy, such that externally triggered stimuli appeared at regular intervals. However, this condition still differs from the action condition in another important process – namely the ability of the participant to control when the stimulus appears – i.e. temporal control. Indeed, the vast majority of studies on sensory attenuation published to date include one of these two conditions as their baseline condition, and therefore rather than being caused by effect specific prediction, these phenomena might simply be caused by increased temporal prediction or temporal control. The importance of adequately controlling temporal prediction is highlighted by a recent study by Vroomen and Stekelenburg (2009), who showed attenuation of the auditory N1 component for a crashing sound emitted when a visual stimulus of a ball was seen to move towards and crash into a central square, compared to the same visual auditory event occurring unpredictably. This suggests that sensory attenuation can occur for predicted sensory events completely independently of action generation.

Similarly, intentional binding is often assessed by asking participants to report the time at which an action triggered tone occurred, as well as the time at which an externally triggered tone occurs (e.g., Haggard et al., 2002). As with the example above concerning sensory attenuation, these conditions differ not only in the presence of an action, but also with the degree to which participants are able to predict the onset of the tone. Even in those experiments that include a sensory cue prior to the onset of the imperative stimulus (e.g., Cravo et al., 2011), the control and experimental conditions differ in terms of the participants' ability to control when the target stimulus will appear. A recent study by Buehner and Humphreys (2010) showed that increased causal belief (i.e., the belief that one event is the origin of another) regarding a sequence of events was sufficient to produce a spatial binding effect, similar to the temporal effect described in intentional binding. Note that in their experiment, no actions were produced, but the attribution of causality to a sequence of events was sufficient to produce binding. If temporal control works in a similar way to increase causal attribution, this may explain intentional binding without the need to invoke effect specific prediction mechanisms.

One important avenue of research to show that predictive action mechanisms drive these phenomena has been to either record or disrupt brain activity during action preparation. Haggard and colleagues have shown that both sensory attenuation (Haggard and Whitford, 2004) and intentional binding (Moore et al., 2010; see Fig. 5) are reduced or abolished when TMS is used to disrupt activity in SMA. Similarly, by recording differences in brain activity in the motor system between actions which produce an effect and those which do not, other studies (e.g., Blakemore et al., 1999b; Hughes and Waszak, 2011) have confirmed that action preparation differs for actions with a predictable sensory effect. However, while these studies show that action preparation is important in sensory attenuation and intentional binding, they do not speak to whether this predictive mechanism involves identity prediction. Perhaps the only way to answer this question is by careful selection of conditions differing only in the process of interest. Cardoso-Leite et al. (2010) showed that sensitivity to near threshold stimuli are reduced when they are congruent with a learnt action-effect contingency. This finding shows that predicting which of two stimuli (oriented Gabor patches) will be presented effects one's sensitivity to the stimulus and provides evidence of action identity prediction as a cause for sensory attenuation. Importantly, they also showed that this change in sensitivity was absent when a concurrent sound (rather than the action) predicted the identity of the visual stimulus, suggesting that motor prediction mechanisms and not simply identity prediction was the cause of sensory attenuation. This finding, along with the findings discussed above regarding chromatic adaptation following learning of effect-specific motor contingencies (Bompas and O'Regan, 2006a,b; Richters and Eskew, 2009) provide preliminary evidence that action identity prediction mechanisms can influence processing of sensory action effects. However, further research isolating this process from mechanisms involving temporal prediction, temporal control and non-motor identity prediction is required to determine the extent to which sensory attenuation and intentional binding are driven by predictive mechanisms that are specific to the action system as well as being sensitive to the specific action-effect relationships.

6. A pre-activation account of sensory attenuation and intentional binding

The caveat summarized in the last section notwithstanding we will now try to bring the elements outlined thus far together. On the whole the following picture seems to emerge: In addition to its various functions related to action control, such as internal action selection, resolution of conflict between different condition-action associations, error processing, and task-set related control, the pMFC is involved in sending an efferent copy of the motor command to posterior regions (Haggard and Whitford, 2004). The precise mechanisms are not yet known and may involve the cerebellum (cf. Bastian, 2006), but, as a consequence of this efference copy, perceptual areas representing the anticipated effect are pre-activated as if it was actually perceived (e.g., Kühn et al., 2010). The detection of a mismatch between anticipated and actual effect triggers processes of error handling: attention is allocated to the unexpected event (as suggested by the larger P3a for unanticipated deviant stimuli; Waszak and Herwig, 2007) and a negative reinforcement signal is transmitted from the mesencephalic dopamine system to the ACC initiating adaptive learning processes (as suggested by the NAE; Band et al., 2009). By contrast, when anticipated and true effect match, the sensory effect of the action is attenuated (e.g., Baess et al., 2008; Cardoso-Leite et al., 2010) and is perceived earlier (the stimulus shift in intentional binding; e.g., Haggard et al., 2002).

Note that the two phenomenological consequences of a match between anticipated and true action effect seem to be somewhat contradicting at first sight: an anticipated action effect is perceived attenuated and earlier. How can this be explained?

The precise mechanism behind sensory attenuation and intentional binding are yet to be discovered. Many studies do not state the precise mechanism involved in sensory attenuation, while some state that the predicted effect is "subtracted" from the actual sensory effect or that the predicted effect is "cancelled", in line with the cancellation model proposed by Von Holst and Mittelstaedt (1950) to explain the stability of the visual scene during eye movements (e.g., Bays et al., 2006; Blakemore et al., 1998; Bays and Wolpert, 2007). In terms of the Signal Detection Theory, this account seems to assume that the mean of the signal distribution is decreased, thus making signal and noise less distinctive and d' smaller. This is also reflected in the fact that the effect is usually called sensory suppression. We chose the term attenuation to avoid any theoretical coloring. As concerns intentional binding it has originally been proposed that events following a voluntary action are "bound by a specific cognitive function of the central nervous system" (Haggard et al., 2002, p. 384) without specifying a particular mechanism that might account for the perceived shift. Ever since research has focused on questions like whether the intentional binding is based on predictive or postdictive mechanisms rather than on an explanation of the phenomenology.

However, we see a possibility that might account for sensory attenuation, chromatic adaptation, and intentional binding (at least as concerns the perceived shift of the stimulus). This account is based on the finding outlined above that the preparation or execution of an action preactivates sensory networks that represent the actions' expected perceptual consequence, as suggested, for example, by the fMRI study from Kühn et al. (2010) who found an increase in activity in the parahippocampal place area (PPA) and fusiform face area (FFA) for actions that in a previous training phase have triggered houses and faces, respectively. We suggest that this preactivation increases the mean level of activity in the perceptual units representing the anticipated effect to some pedestal level. In terms of the signal detection theory, as described above (Green and Swets, 1966), the sensitivity loss observed for anticipated action effects can be explained by discrimination of the signal activation from the pedestal level being more difficult than discrimination of the signal activation from the noise baseline level (i.e., in conditions, in which baseline activity in the neurons coding the action effect is not raised due to effect anticipation). This preactivation account contrasts with the suppression account in that d' for anticipated effects is reduced due to an increased mean of the baseline distribution and not because the mean of the signal distribution is decreased. Fig. 6 illustrates the preactivation account. For details see figure caption.

Evidently, a preactivation as described above does not only increase the mean of the noise distribution (i.e., the distribution of the internal response if no stimulus is presented), but also the mean of the signal distribution (i.e., the distribution of the internal response if a stimulus is presented). However, notice that the higher the pre-stimulus activation level, the smaller the effect of the stimulus on the internal response. (Imagine that the pre-stimulus activation is maximal: all units are active; in that case the stimulus would not have any additional effect at all). In other words, the stimulus increases the internal response less when added to the preactivation baseline (from panels d to e in Fig. 6), than when added to the noise baseline without preactivation (from panels a to b in Fig. 6). As a consequence, the preactivation brings about that the means of both signal and noise distributions are increased, but the difference between them (d') is decreased.

At first glance such a pre-activation account might seem at odds with ERP studies that show attenuation of sensory responses to selfgenerated stimuli. Since the level of the internal response is greater with anticipation (see Fig. 6) one might expect ERP signals to also be greater when pre-activation is present – the opposite of sensory attenuation. However, all those ERP studies described above include a baseline period immediately prior to the onset of the stimulus. Closer examination of Fig. 6 reveals that although the overall activation is greater with pre-activation, removing the activity prior to the onset of the stimulus for both conditions – the equivalent of applying a baseline to an ERP – would result in a reduced sensory response for the self-generated actions. In cases where the



Fig. 6. The preactivation account of the sensory attenuation effect. The figure illustrates sensory attenuation as assessed in the study of Cardoso-Leite et al. (2010), i.e., using newly learned action effects and signal detection methodology. The upper row of panels shows the hypothetical internal response during a typical trial, that is, the activity in (groups of) neurons coding the to-be-detected stimulus, before the stimulus has been associated to the action. The lower row of panels show the internal response after the observer has undergone a learning phase during which an action (e.g., a right hand key press) is systematically followed by a specific visual stimulation (e.g., a 45° oriented Gabor patch). The x-axis in panels a, b and d, e represents time with the onset of relevant events being indicated by black vertical dashed lines and icons (finger press and Gabor patch). The y-axis in all panels represents the magnitude of the internal response. For illustrative purposes only we will assume that in order to decide whether a stimulus was present or not on a given trial, participants will use the maximum of the internal response within a certain time window (the areas shaded in gray in panels a, b and d, e). The x-axis in panels c and f refer to the probability of observing a particular value of this maximal internal response. (a) Prior to the learning phase, a motor action does not affect the internal response (black curve), (b) a visual stimulation however does (blue curve). Panel (c) illustrates the distribution of the maximum of the internal responses for both signal present (blue curve) and signal absent (black curve) trials. The participants' task is to determine on each trial for a given internal response which of these situations is more likely to have occurred ("stimulus present or not?"). The performance in this task depends on how far apart these two curves are and can be characterized in terms of d' (the distance between the means of the two distributions, as highlighted by a blue vertical line). (d) After the learning phase, an action will by itself produce an increase of internal response (gray curve). (e) When a stimulus is presented subsequently to the action, the stimulus induced increase will be added to the action-induced preactivation. However, due to the higher pre-stimulus activation, the stimulus-induced increase is smaller than without pre-activation (panel b). (f) represents, just as panel c, the distribution of maximal internal responses during the relevant time interval. The red curve represents the distribution of internal responses for a motor action followed by the associated stimulus whereas the gray curve shows the distribution of internal responses when only the action occurs. Again the performance in this situation can be assessed in terms of d' (red vertical line). The comparison of panels c and f demonstrates the reduction in sensitivity (d') after the learning phase that characterizes the sensory attenuation phenomenon. This reduction in d' is illustrated by the signal and noise distributions being less different after the association phase (red and gray curves in panel c) than before (black and blue curves in panel f).

pre-activation might not occur immediately prior to target onset, ERP attenuation may be accounted for by similar mechanisms to those present for repitition suppression (see detailed discussion below). As such, although somewhat counterintuitive, the preactivation account provides a plausible explanation for previously observed attenuated ERP responses to self-generated stimuli.

Chromatic adaptation after eye or joystick movements (see above; Bompas and O'Regan, 2006a,b; Richters, 2008; Richters and Eskew, 2009) could be explained along the same lines. If a particular movement entails activity coding for the anticipated color, then a yellow patch looks greenish after a movement associated with a red stimulus because the red input is "attenuated" due to an increased baseline for "red" (such that the red component of the yellow stimulus has a smaller effect). At the same time, the preactivation model can also account for the shift of the perceived onset time of anticipated sensory action consequences (see Fig. 7). An action effect might reach the threshold of awareness faster, if the activity in its neural representation starts from the pedestal level than when it starts from the baseline level. Thus, signal accumulation for non-anticipated stimuli takes longer to reach the threshold of awareness than signal accumulation for anticipated action effects, since the perceptual representation of the latter has already been pre-activated by internal motor signals. One might argue that this account cannot explain the shift of the perception of the movement regularly observed in experiments on intentional binding (e.g., Haggard et al., 2002). However, binding effects of the movement and of the sensory may be based on different mechanisms. This notion is in agreement with

Without anticipation (e.g. before the association)

Without anticipation (e.g. before the association)



With anticipation (e.g. after the association)



Fig. 7. Illustration of the preactivation account of the perceived shift of stimulus onset in intentional binding. The moment of conscious detection of a stimulus is modeled as the point in time where the magnitude of the internal response (i.e., the activity in (groups of) neurons coding the to-be-detected stimulus) reaches a critical value (the threshold). (a) Prior to the learning phase an action followed by a visual stimulus will produce the same internal response as the stimulus alone (blue curve). This response, if strong enough, will at some point reach a threshold (black vertical line) and so cause participants to perceive the stimulus. Perceptual latency is defined as the duration separating the onset of the visual stimulus (indicated by a black vertical dashed line) and the moment of detection. (b) After the learning phase, the internal response will start increasing during action preparation and, thus, will be elevated at the moment when the stimulus induced increase in internal response starts. As a consequence, at the moment of stimulus presentation, the internal response has a head start in its race towards the threshold. The moment the threshold is reached is indicated by a red vertical line. The comparison of the perceptual latencies in panels (a and b) show that the onset of the stimulus will be perceived earlier with than without preactivation. Indeed the perceptual latency after the learning phase (illustrated as a red horizontal bar at the bottom of the figure) is much shorter than the perceptual latency before the learning occurred (blue horizontal bar).

a recent study by Moore et al. (2010). These authors showed that a disruption of pre-SMA function by TMS (transcranial magnetic stimulation) affected the perception of the onset of the sensory effect but not of the perception of movement onset (see Fig. 5). Likewise, Desantis et al. (2011) report a top-down effect of the participants' causal beliefs on the perceived shift of the stimulus, but not on the shift of the movement.

In a nutshell, the preactivation account explains sensory attenuation because the activation due to the anticipation of the action effect constitutes an increased baseline from which the signal is less discriminable than from the baseline without effect anticipation. It explains the shift in perceived onset of anticipated action effects because the increased baseline gives the anticipated effect a headstart. Fig. 6 illustrates the pre-activation model.

7. Similarities between action effect anticipation and imagery

The notion that internal effect anticipation entails activity in perceptual areas that represent the anticipated effect bears some resemblance to perceptually based theories of imagery (e.g., Kosslyn et al., 2001; Pearson et al., 2008; for a review see Kaski, 2002). These theories assume that 'seeing with the mind's eye' or 'hearing with the mind's ear' engages at least partially the same brain mechanisms that are used in perception. A large body of evidence has been accumulated showing that when the internal representations of stimuli have to be maintained over time or reevoked in the absence of any external stimulation perceptual areas on many levels of processing are active. There is evidence that even very early visual areas are involved (see for example Kosslyn et al., 1999, but see Roland and Gulyas, 1994, 1995). As concerns higher visual areas, O'Craven and Kanwisher (2000) found activity in FFA and PPA during mental imagery of faces and scenes, respectively (see also Johnson et al., 2007; Druzgal and D'Esposito, 2003). That mental imagery is based on sensory process has also been shown in the somatosensory domain. Using fMRI, Carlsson et al. (2000) compared neural activation during the perception of a somatosensory stimulus ("tickling") and in anticipation of the same sensory event (Carlsson et al., 2000). Carlsson et al. observed that activations and deactivations during anticipation and perception were similar. All these observations are in line with the view that evoking and maintaining internal representations of stimuli entails top-down modulation of activity in perceptual cortical regions initially activated during the perception of these stimuli.

Interestingly, it has been repeatedly shown that internal images and true percepts interact. In 1910 Perky made a curious observation: when participants imagined seeing an object (for example a banana) while looking at a supposedly blank screen, on which was actually projected a faint picture of that object, participants had difficulties seeing it. This reduction in performance from the no-imagery to the imagery condition is now known as the Perky effect. The Perky effect has been confirmed using more modern techniques (e.g., Craver-Lemley and Reeves, 1987; Craver-Lemley et al., 1997). It has been found that the Perky effect can be quite stimulus-specific. Finke (1986) studied interactions between mental imagery and perception by assessing detection reaction times, amongst other measures, in response to bar patterns presented at orientations 90° apart. Detection reaction times and error rates were increased when the imagined bars were aligned with the target bars, providing further evidence that pre-activation of sensory areas by imagery can reduce perceptual sensitivity.

In the light of the striking similarity between the Perky effect and the sensory attenuation, it is of course tempting to speculate that they are essentially based on the same mechanism. For example, the reason why Cardoso-Leite et al. (2010) observed reduced detection d'–s for Gabor patches if the anticipated and observed action effect were congruent might be the same reason why Finke (1986) observed reduced detection reaction times for congruent image-percept combinations using bar stimuli. More specifically, action effect anticipation and mental imagery produce activity in perceptual networks, mimicking a reduction in target intensity and, thus, resulting in sensory interference.

We would like to point out that some studies suggest that, far from causing a Perky effect, i.e. interference, mental imagery actually facilitates perception. For example, Farah (1985) observed that evoking the internal representation of a letter enhances the detection of that same letter. Likewise, Finke (1986) reported in the same study mentioned above that, contrary to detection d'-s, discrimination d'-s are increased for congruent image-percept combinations. Thus the precise nature of when mental imagery interferes with or facilitates perception may require further clarification. However, as mentioned above, sensory attenuation and the shift in the perceived time of the stimulus in intentional binding are also somewhat paradoxical. We believe that a better understanding of how internally evoked perceptual representations interact with perception – resulting in interference or facilitation – could provide useful insights into the phenomenological consequences of effect anticipation.

8. Repetition suppression as a neural basis of the perceptual consequences of action effect anticipation?

Above we outlined how the phenomenological consequences of effect anticipation, especially sensory attenuation, could be explained in terms of a preactivation of perceptual units coding for the anticipated effect. However, an important question that we have only briefly discussed thus far is how this model might explain neural sensory suppression measured by means of ERPs and fMRI (e.g., Blakemore et al., 1998, 2000; but see Section 5 for an assessment of these effects).

We believe that the answer to this question is related to a phenomenon that has widely been studied in research on perceptual representations: a wealth of literature has demonstrated that when stimuli are repeated neural activity is reduced (for review see Grill-Spector et al., 2006). This stimulus-specific decrease in activity across stimulus repetition has most commonly been referred to as repetition suppression.

Repetition suppression has been demonstrated with single-cell recordings in monkeys (Miller et al., 1993), as well as in humans using fMRI (see Kourtzi and Grill-Spector, 2005) and EEG/MEG (Henson et al., 2004). It has been found in various areas in the brain, including in the ventral temporal cortex, medial temporal and frontal cortex. For example, it has been demonstrated in FFA in response to repeated face stimuli (e.g., Henson and Mouchlianitis, 2007).

At least three models have been proposed in the literature to account for neural repetition suppression (see Grill-Spector et al., 2006). The sharpening model assumes that repetition suppression is due to a repeated stimulus being represented more sparsely, because the firing rate of neurons responding to irrelevant features decreases across repetitions. According to the facilitation model, repetition suppression is due to stimuli being processed more quickly when presented more than once (i.e., neurons firing for a shorter period of time). The fatigue model, finally, suggests that repetition suppression results from neurons being less responsive when a stimulus is repeated due to firing rate adaptation and synaptic depression. Grill-Spector et al. (2006) speculate that the different models explain repetition suppression at different time scales, with the sharpening model and the facilitation model accounting for long-term repetition suppression across intervening trials and the fatigue model accounting for short-lived repetition suppression that operates within a few hundred milliseconds after immediate repetitions of a stimulus.

We suggest that neural sensory suppression of self-produced stimuli (i.e. anticipated action effects) is based on similar if not identical neural mechanisms as repetition suppression. If action effect anticipation, as suggested by the preactivation account, entails activity similar to the activity that results from the true perception of the given stimulus, then the activity triggered by a correctly anticipated action effect is actually the repetition of the anticipation-based activity. As a consequence, a correctly anticipated action effect should be subject to the same neural dynamics as a stimulus that is truly repeated, at least to a certain degree. Neural sensory suppression as measured with EEG and fMRI (see above) could, thus, be due to neural sharpening, facilitation and/or fatigue.

Note that the fatigue model is perhaps the most compatible with the preactivation account outlined above. This is because fatigue of neurons (or fatigue in a network of neurons) coding for a stimulus is basically equivalent to an increase of the baseline activity as described above (see Fig. 6): A neuron that has been preactivated as a consequence of internal effect anticipation is not available to code for the same stimulus when the true action effect appears; according to a preactivation account in the strict sense of the word, it is not available because it is already active; according to a fatigue account, it is not available because its excitability is decreased. In both accounts, repetition/sensory suppression is due to the preactivation slightly increasing the saturation in the network coding for the stimulus.

9. Conclusions and outlook

We have summarized and integrated experimental evidence demonstrating that the pMFC and the cerebellum are involved in the anticipation of sensory action effects and that this anticipation entails activity in perceptual areas coding for the anticipated effect. Furthermore, we have shown that a mismatch between anticipated and true action effect triggers processes of error handling, whereas a match results in phenomenological consequences like sensory attenuation and intentional binding. Finally, we have shown how a simple model based on the preactivation of the perceptual representation of the anticipated effect can account for most of the phenomenological consequences that voluntary action has on the perception of its sensory effects, in particular sensory attenuation, chromatic adaptation as well as intentional binding. However, the preactivation account also offers inherently straightforward interpretation of the most thoroughly investigated neural consequence of action effect anticipation, namely the attenuated neural response to a predicted action effect.

Clearly, many questions remain regarding the functional and neurophysiological underpinnings of effect anticipation. Regarding the processing of incorrectly anticipated effects, more research is needed to understand how attentional and error processing relate, and how they warrant efficient action-effect learning and a smooth agent-environment interaction. Regarding the processing of correctly anticipated effects, extremely informative will be the concurrent assessment of neural and perceptual indices of sensory attenuation. This will allow us to differentiate between truly perceptual and other, for example attentional, aspects of effect anticipation and to understand possible differences between sensory domains. Progress will also be made studying in more detail how and on which levels effect anticipation entails preactivation of perceptual representations. Investigating the relationship between effect anticipation and mental imagery in general will be fruitful. Another promising avenue for future research could be to determine the degree to which repetition suppression effects co-vary with sensory attenuation effects for example by assessing the specificity of the prediction or repetition or by comparing the relative time courses of the two phenomena. Last but not least, future research should also try to integrate knowledge from the vast literature on multisensory integration (e.g., Calvert et al., 2000; Calvert, 2001). After all, real action effects are usually multisensory and not unimodal as in most laboratory experiments. This future research will help validating or refuting the theoretical framework outlined in this review.

References

- Aliu, S.O., Houde, J.F., Nagarajan, S.S., 2009. Motor-induced suppression of the auditorycortex. Journal of Cognitive Neuroscience 21 (4), 791–802.
- Amiez, C., Joseph, J.P., Procyk, E., 2006. Reward encoding in the monkey anterior cingulate cortex. Cerebral Cortex 16 (7), 1040–1055.
- Baess, P., Jacobsen, T., Schroger, E., 2008. Suppression of the auditory N1 eventrelated potential component with unpredictable self-initiated tones: evidence for internal forward models with dynamic stimulation. International Journal of Psychophysiology 70 (2), 137–143.
- Baess, P., Widmann, A., Roye, A., Schroger, E., Jacobsen, T., 2009. Attenuated human auditory middle latency response and evoked 40-Hz response to self-initiated sounds. European Journal of Neuroscience 29 (7), 1514–1521.
- Balleine, B.W., Dickinson, A., 1998. Goal-directed instrumental action: contingency and incentive learning and their cortical substrates. Neuropharmacology 37, 407–419.
- Balleine, B.W., O'Doherty, J.P., 2010. Human and rodent homologies in action control: corticostriatal determinants of goal-directed and habitual action. Neuropsychopharmacology 35, 48–69.
- Band, G.P.H., van Steenbergen, H., Ridderinkhof, K.R., Falkenstein, M., Hommel, B., 2009. Action-effect negativity: irrelevant action effects are monitored like relevant feedback. Biological Psychology 82, 211–218.
- Bastian, A.J., 2006. Learning to predict the future: the cerebellum adapts feedforward movement control. Current Opinion in Neurobiology 16 (6), 645–649.
- Bayne, T., Pacherie, E., 2007. Narrators and comparators: the architecture of agentive selfawareness. Synthese 159, 475–491.
- Bays, P.M., Wolpert, D.M., Flanagan, J.R., 2005. Perception of the consequences of self-action is temporally tuned and event driven. Current Biology 15 (12), 1125–1128.
- Bays, P.M., Flanagan, J.R., Wolpert, Daniel, M., 2006. Attenuation of self-generated tactile sensations is predictive, not postdictive. PLoS Biology 4 (2), e28.
- Bays, P.M., Wolpert, D.M., 2007. Predictive attenuation in the perception of touch. In: Haggard, P., Rossetti, Y., Kawato, M. (Eds.), Sensorimotor Foundations of Higher Cognition, Attention and Performance. Oxford University Press, Oxford, England, pp. 339–358.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 1999a. Spatio-temporal prediction modulates the perception of self-produced stimuli. Journal of Cognitive Neuroscience 11 (5), 551–559.
- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 1999b. The cerebellum contributes to somatosensory cortical activity during self-produced tactile stimulation. Neuroimage 10 (4), 448–459.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 2001. The cerebellum is involved in predicting the sensory consequences of action. NeuroReport 12 (9), 1879–1884.
- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 1998. Central cancellation of self-produced tickle sensation. Nature Neuroscience 1 (7), 635–640.
- Blakemore, S.J., Wolpert, D., Frith, C., 2000. Why can't you tickle yourself? NeuroReport 11 (11), R11–R16.
- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 2002. Abnormalities in the awareness of action. Trends Cognitive Science 6 (6), 237–242.
- Bompas, A., O'Regan, J.K., 2006a. Evidence for a role of action in color perception. Perception 35, 65–78.
- Bompas, A., O'Regan, J.K., 2006b. More evidence for sensorimotor adaptation in color perception. Journal of Vision 6 (2), 145–153.
- Botvinick, M.M., 2007. Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. Cognitive, Affective & Behavioral Neuroscience 7 (4), 356–366.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychological Review 108 (3), 624– 652.
- Brass, M., von Cramon, D.Y., 2002. The role of the frontal cortex in task preparation. Cerebral Cortex 12, 908–914.
- Buehner, M.J., Humphreys, G.R., 2009. Causal binding of actions to their effects. Psychological Science 20 (10), 1221–1228.
 Buehner, M.J., Humphreys, G.R., 2010. Causal contraction: spatial binding in the
- Buehner, M.J., Humphreys, G.R., 2010. Causal contraction: spatial binding in the perception of collision events. Psychological Science 21 (1), 44–48.
- Calvert, G.A., Campbell, R., Brammer, M.J., 2000. Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. Current Biology 10 (11), 649–657.
- Calvert, G.A., 2001. Crossmodal processing in the human brain: insights from functional neuroimaging studies. Cerebral Cortex 11 (12), 1110–1123.
- Cardoso-Leite, P., Mamassian, P., Schütz-Bosbach, S., Waszak, F., 2010. A new look at sensory attenuation: action–effect anticipation affects sensitivity, not response bias. Psychological Science 21 (12), 1740–1745.
- Carlsson, K., Petrovic, P., Skare, S., Petersson, K.M., Ingvar, M., 2000. Tickling expectations: neural processing in anticipation of a sensory stimulus. Journal of Cognitive Neuroscience 12 (4), 691–703.
- Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., Cohen, J.D., 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. Science 280 (5364), 747–749.
- Coles, M.G., 1989. Modern mind-brain reading: psychophysiology, physiology, and cognition. Psychophysiology 26 (3), 251–269.
- Craver-Lemley, C., Reeves, A., 1987. Visual imagery selectively reduces vernier acuity. Perception 16, 599–614.
- Craver-Lemley, C., Reeves, A., Arterberry, M.E., 1997. Effects of imagery on vernier acuity under conditions of induced depth. Journal of Experimental Psychology: Human Perception and Performance 23, 3–13.

- Cravo, A.M., Claessens, P.M., Baldo, M.V., 2011. The relation between action, predictability and temporal contiguity in temporal binding. Acta Psychologica (Amst) 136 (1), 157–166.
- Crone, E.A., Wendelken, C., Donohue, S.E., Bunge, S.A., 2006. Neural evidence for dissociable components of task-switching. Cerebral Cortex 16, 475–486.
- Cunnington, R., Windischberger, C., Moser, E., 2005. Premovement activity of the pre-supplementary motor area and the readiness for action: studies of timeresolved event-related functional MRI. Human Movement Science 24, 644–656.
- Cunnington, R., Windischberger, C., Deecke, L., Moser, E., 2002. The preparation and execution of self-initiated and externally-triggered movement: a study of eventrelated fMRI. Neuroimage 15 (2), 373–385.
- Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D.Y., Engel, A.K., 2005. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. Journal of Neuroscience 25 (50), 11730–11737.
- Dehaene, S., Posner, M.I., Tucker, D.M., 1994. Localization of a neural system for error detection and compensation. Psychological Science 5 (5), 303–305.
- Del Cul, A., Baillet, S., Dehaene, S., 2007. Brain dynamics underlying the nonlinear threshold for access to consciousness. PLoS Biolology 5 (10), e260.
- Desantis, A., Roussel, C., Waszak, F., 2011. On the influence of causal beliefs on the feeling of agency. Consciousness and Cognition 20 (4), 1211–1220, doi:10.1016/j.concog.2011.02.012.
- Druzgal, T.J., D'Esposito, M., 2003. Dissecting contributions of prefrontal cortex and fusiform face area to face working memory. Journal of Cognitive Neuroscience 15, 771–784.
- Elsner, B., Hommel, B., Mentschel, C., Drzezga, A., Prinz, W., Conrad, B., Siebner, H., 2002. Linking actions and their perceivable consequences in the human brain. Neuroimage 17, 364–372.
- Elsner, B., Hommel, B., 2001. Effect anticipation and action control. Journal of Experimental Psychology: Human Perception and Performance 27 (1), 229–240.
- Engbert, K., Wohlschlager, A., Haggard, P., 2008. Who is causing what? The sense of agency is relational and efferent-triggered. Cognition 107 (2), 693–704.
- Engbert, K., Wohlschlager, A., Thomas, R., Haggard, P., 2007. Agency, subjective time, and other minds. Journal of Experimental Psychology: Human Perception and Performance 33 (6), 1261–1268.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. Nature 392 (6676), 598-601.
- Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1990. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, C.H.M., Gaillard, A.W.K., Kok, A. (Eds.), Psychophysiological Brain Research. Tilburg University Press, Tilburg, The Netherlands, pp. 192–195.
- Farah, M.J., 1985. Psychophysical evidence for a shared representational medium for mental images and percepts. Journal of Experimental Psychology: General (14), 91–103.
- Finke, R.A., 1986. Some consequences of visualization in pattern identification and detection. The American Journal of Psychology 99 (2), 257–274.
- Friedman, D., Cycowicz, Y.M., Gaeta, H., 2001. The novelty P3: an event-related brain potential (ERP) sign of the brain's evaluation of novelty. Neuroscience and Biobehavioral Reviews 25 (4), 355–373.
- Frith, C., 2005. The self in action: lessons from delusions of control. Consciousness and Cognition 14 (4), 752–770.
- Frith, C.D., Blakemore, S.-J., Wolpert, D.M., 2000. Abnormalities in the awareness and control of action. Philosophical Transactions of the Royal Society of London B 355, 1771–1788.
- Gomes, G., 2002. The interpretation of Libet's results on the timing of conscious events: a commentary. Consciousness and Cognition 11, 221–230.
- Green, D.M., Swets, J.A., 1966. Signal Detection Theory and Psychophysics. New York, NY, Wiley.
- Greenwald, A., 1970. Sensory feedback mechanisms in performance control: with special reference to the ideomotor mechanism. Psychological Review 77, 73–99.
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends in Cognitive Sciences 10 (1), 14–23.
- Haggard, P., Clark, S., Kalogeras, J., 2002. Voluntary action and conscious awareness. Nature Neuroscience 5, 382–385.
- Haggard, P., Clark, S., 2003. Intentional action: conscious experience and neural prediction. Consciousness and Cognition 12, 695–707.
- Haggard, P., Whitford, B., 2004. Supplementary motor area provides an efferent signal for sensory suppression. Cognitive Brain Research 19 (1), 52–58.
- Haggard, P., Cole, J., 2007. Intention, attention and the temporal experience of action. Consciousness and Cognition 16 (2), 211–220.
- Haggard, P., 2008. Human volition: towards a neuroscience of will. Nature Reviews Neuroscience 9 (12), 934–946.
- Harleß, E., 1861. Der Apparat des Willens. Zeitschrift fuer Philosophie und Philosophische Kritik 38, 50–73.
- Henson, R.N., Rylands, A., Ross, E., Vuilleumeir, P., Rugg, M.D., 2004. The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. Neuroimage 21, 1674–1689.
- Henson, R.N., Mouchlianitis, E., 2007. Effect of spatial attention on stimulus-specific haemodynamic repetition effects. NeuroImage 35 (3), 1317–1329.
- Herwig, A., Prinz, W., Waszak, F., 2007. Two modes of sensorimotor integration in intention-based and stimulus-based action. Quarterly Journal of Experimental Psychology A: Human Experimental Psychology 60 (11), 1540–1554.
- Holmes, N.M., Marchand, A.R., Coutureau, E., 2010. Pavlovian to instrumental transfer: a neurobehavioural perspective. Neuroscience and Biobehavioral Reviews 34, 1277–1295.

- Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychological Review 109, 679–709.
- Hommel, B., Müsseler, J., Aschersleben, G., Prinz, W., 2001. The theory of event coding (TEC): a framework for perception and action planning. Behavioral and Brain Sciences 24, 849–937.
- Hughes, G., Waszak, F., 2011. ERP correlates of action effect prediction and visual sensory attenuation in voluntary action. NeuroImage 56 (3), 1632–1640.
- Humphreys, G.R., Buehner, M.J., 2009. Magnitude estimation reveals temporal binding at super-second intervals. Journal Experimental Psychology: Human Perception & Performance 35 (5), 1542–1549.
- James, W., 1890. The Principles of Psychology, vol. 2. Dover Publications, New York. Jameson, D., Hurvich, L.M., 1972. Color adaptation: sensitivity, contrast, after-
- Jameson, D., Hurvich, LW., 1972. Color adaptation. sensitivity, contrast, arterimages. In: Jameson, D., Hurvich, LM. (Eds.), Handbook of Sensory Physiology, vol. 7. Springer, New York, pp. 568–581.
- Johnson, M.R., Mitchell, K.J., Raye, C.L., D'Esposito, M., Johnson, M.K., 2007. A brief thought can modulate activity in extrastriate visual areas: top-down effects of refreshing just-seen visual stimuli. NeuroImage 37, 290–299.
- Kanwisher, N.G., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. Journal of Neuroscience 17, 4302–4311.
- Kaski, D., 2002. Revision: is visual perception a requisite for visual imagery? Perception 31 (6), 717–731.
- Kerns, J.G., Cohen, J.D., MacDonald III, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303, 1023–1026.
- Killcross, S., Coutureau, E., 2003. Coordination of actions and habits in the medial prefrontal cortex of rats. Cerebral Cortex 13, 400–408.
- Kosslyn, S.M., Pascual-Leone, A., Felician, O., et al., 1999. The role of area 17 in visual imagery: convergent evidence from PET and rTMS. Science 284, 167– 170.
- Kosslyn, S.M., Ganis, G., Thompson, W.L., 2001. Neural foundations of imagery. Nature Reviews Neuroscience 2, 635–642.
- Kourtzi, Z., Grill-Spector, K., 2005. fMRI adaptation: a tool for studying visual representations in the primate brain. In: Rhodes, G., Clifford, C.W.G. (Eds.), Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision. Oxford University Press, pp. 173–188.
- Krieghoff, V., Brass, M., Prinz, W., Waszak, F., 2009. Dissociating what and when of intentional actions. Frontiers in Human Neuroscience 3/3, 1–10.
- Krieghoff, V., Waszak, F., Prinz, W., Brass, M., 2011. Neural and behavioral correlates of intentional actions. Neuropsychologia 49 (5), 767–776.
- Kühn, S., Brass, M., 2010. Planning not to do something: does intending not to do something activate associated sensory consequences? Cognitive, Affective and Behavioural Neuroscience 10 (4), 454–459.
- Kühn, S., Keizer, A., Rombouts, S.A., Hommel, B., 2011. The functional and neural mechanism of action preparation: roles of EBA and FFA in voluntary action control. Journal of Cognitive Neuroscience 23 (1), 214–220.
- Kühn, S., Seurinck, R., Fias, W., Waszak, F., 2010. The internal anticipation of sensory action effects: when action induces FFA and PPA activity. Frontiers in Human Neuroscience 4/54, 1–7.
- Kunde, W., 2001. Response-effect compatibility in manual choice reaction tasks. Journal of Experimental Psychology: Human Perception and Performance 27 (2), 387–394.
- Kunde, W., 2003. Temporal response-effect compatibility. Psychological Research 67, 153-159.
- Leuthold, H., Jentzsch, I., 2002. Distinguishing neural sources of movement preparation and execution. An electrophysiological analysis. Biological Psychology 60 (2–3), 173–198.
- Libet, B., Gleason, C.A., Wright, E.W., Pearl, D.K., 1983. Time of conscious intention to act in relation to onset of cerebral activity (readiness potential): the unconscious initiation of a freely voluntary act. Brain 106, 623–642.
- Liston, C., Matalon, S., Hare, T.A., Davidson, M.C., Casey, B.J., 2006. Anterior cingulate and posterior parietal cortices are sensitive to dissociable forms of conflict in a task-switching paradigm. Neuron 50, 643–653.
- Lotze, R.H., 1852. Medicinische Psychologie oder die Physiologie der Seele. Weidmann'sche Buchhandlung, Leipzig.
- Matsumoto, K., Suzuki, W., Tanaka, K., 2003. Neuronal correlates of goal-based motor selection in the prefrontal cortex. Science 301 (5630), 229–232.
- Melcher, T., Weidema, M., Eenshuistra, R.M., Hommel, B., Gruber, O., 2008. The neural substrate of the ideomotor principle: an event-related fMRI analysis. Neuroimage 39 (3), 1274–1288.
- Menon, V., Adleman, N.E., White, C.D., Glover, G.H., Reiss, A.L., 2001. Error-related brain activation during a Go/NoGo response inhibition task. Human Brain Mapping 12 (3), 131–143.
- Miall, R.C., Wolpert, D.M., 1996. Forward models for physiological motor control. Neural Networks 9 (8), 1265–1279.
- Miller, E.K., Li, L., Desimone, R., 1993. Activity of neurons in anterior inferior temporal cortex during a short-term memory task. Journal of Neuroscience 13, 1460–1478.
- Miltner, W.H.R., Braun, C.H., Coles, M.G.H., 1997. Event-related potentials following incorrect feedback in a time-estimation task: evidence for a 'generic' neural system for error detection. Journal of Cognitive Neuroscience 9, 788–798.
- Moore, J., Haggard, P., 2008. Awareness of action: inference and prediction. Consciousness and Cognition 17, 136–144.
- Moore, J., Lagnado, D., Darvany, D., Haggard, P., 2009a. Feeling of control: contingency determines experience of action. Cognition 110, 279–283.

- Moore, J.W., Wegner, D.M., Haggard, P., 2009b. Modulating the sense of agency with external cues. Consciousness and Cognition 18, 1056–1064.
- Moore, J.W., Ruge, D., Wenke, D., Rothwell, J., Haggard, P., 2010. Disrupting the experience of control in the human brain: pre-supplementary motor area contributes to the sense of agency. Proceedings of the Royal Society – Biological Sciences 277 (1693), 2503–2509.
- Morton, S.M., Bastian, A.J., 2006. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. Journal Neuroscience 26 (36), 9107–9116.
- Mueller, V.A., Brass, M., Waszak, F., Prinz, W., 2007. The role of the preSMA and the rostral cingulate zone in internally selected actions. NeuroImage 37 (4), 1354–1361.
- Näätänen, R., 1990. The role of attention in auditory information processing as revealed by event-related potentials and other measures of cognitive function. Behavioral and Brain Sciences 13, 201–232.
- Nachev, P., Kennard, C., Husain, M., 2008. Functional role of the supplementary and pre-supplementary motor areas. Nature Reviews Neuroscience 9 (11), 856– 869.
- Nattkemper, D., Ziessler, M., Frensch, P., 2010. Binding in voluntary action control. Neuroscience and Biobihavioral Reviews 34, 1092–1101.
- Nittono, H., 2006. Voluntary stimulus production enhances deviance processing in the brain. International Journal of Psychophysiology 59, 15–21.
- Nittono, H., Hamada, A., Hori, T., 2003. Brain potentials after clicking a mouse: a new psychophysiological approach to human-computer interaction. Human Factors 45, 591–599.
- Nittono, H., Ullsperger, P., 2000. Event-related potentials in a self-paced novelty oddball task. NeuroReport 11, 1861–1864.
- O'Craven, K., Kanwisher, N., 2000. Mental imagery of faces and places activates corresponding stimulus-specific brain regions. Journal Cognitive Neuroscience 12, 1013–1023.
- Pacherie, E., 2008. The phenomenology of action: a conceptual framework. Cognition 107 (1), 179–217.
- Passingham, R.E., Bengtsson, S.L., Lau, H.C., 2010. Medial frontal cortex: from selfgenerated action to reflection on one's own performance. Trends in Cognitive Sciences 14 (1), 16–21.
- Pearson, J., Clifford, C.W.G., Tong, F., 2008. The functional impact of mental imagery on conscious perception. Current Biology 18 (13), 982–986.
- Picard, N., Strick, P.L., 1996. Motor areas of the medial wall: a review of their location and functional activation. Cerebral Cortex 6 (3), 342–353.
- Posner, M., Petersen, S., 1990. The attention system of the human brain. Annual Review of Neuroscience 13, 25–42.
- Prinz, W., 1997. Perception and action planning. European Journal of Cognitve Psychology 9, 129–154.
- Prinz, W., Hommel, B. (Eds.), 2002. Common mechanisms in perception and action: attention and performance XIX. Oxford University Press, Oxford.
- Prinz, W., 1990. A common coding approach to perception and action. In: Neumann, O., Prinz, W. (Eds.), Relationships Between Perception and Action. Springer, Berlin, pp. 167–201.
- Richters, D.P., Eskew, R.T., 2009. Quantifying the effect of natural and arbitrary sensorimotor contingencies on chromatic judgments. Journal of Vision 9, 1–11.
- Richters, D.P., 2008. Hand-Eye Correlation: An Arbitrary Sensorimotor Contingency can Alter Visual Sensitivity. Unpublished Ph.D. Thesis.
- Roland, P.E., Gulyas, B., 1994. Visual imagery and visual representation. Trends in Neurosciences 17, 294–296.
- Roland, P.E., Gulyas, B., 1995. Visual memory, visual imagery, and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography. Cerebral Cortex 1, 79–93.
- Rosenbaum, D.A., 2005. The Cinderella of psychology the neglect of motor control in the science of mental life and behavior. American Psychologist 60, 308–317.
 Rushworth, M.F., Hadland, K.A., Paus, T., Sipila, P.K., 2002. Role of the human medial
- Rushworth, M.F., Hadland, K.A., Paus, T., Sipila, P.K., 2002. Role of the human medial frontal cortex in task switching: a combined fMRI and TMS study. Journal of Neurophysiology 87, 2577–2592.
- Rushworth, M.F.S., Walton, M.E., Kennerley, S.W., Bannerman, D.M., 2004. Action sets and decisions in the medial frontal cortex. Trends in Cognitive Sciences 8 (9), 410–417.
- Rushworth, M.F.S., Buckley, M.J., Behrens, T.E.J., Walton, M.E., Bannerman, D.M., 2007. Functional organization of the medial frontal cortex. Current Opinion in Neurobiology 17 (2), 220–227.
- Sato, A., 2008. Action observation modulates auditory perception of the consequence of others' actions. Consciousness and Cognition 17 (4), 1219–1227.
- Sato, A., Yasuda, A., 2005. Illusion of sense of self-agency: discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of ownership. Cognition 94, 241–255.
- Schäfer, E.W., Marcus, M.M., 1973. Self-stimulation alters human sensory brain responses. Science 181 (95), 175–177.
- Schütz-Bosbach, S., Prinz, W., 2007. Perceptual resonance: action-induced modulation of perception. Trends Cognitive Sciences 11, 349–355.
- Shergill, S.S., Bays, P.M., Frith, C.D., Wolpert, D.M., 2003. Two eyes for an eye: the neuroscience of force escalation. Science 301 (5630), 187.
- Shin, Y.K., Proctor, R.W., Capaldi, E.J., 2010. A review of contemporary ideomotor theory. Psychological Bulletin 136 (6), 943–974.
- Swick, D., Turken, A.U., 2002. Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. Proceedings of the National Academy of Sciences of the United States of America 99 (25), 16354–16359.
- Synofzik, M., Vosgerau, G., Newen, A., 2008. Beyond the comparator model: a multifactorial two-step account of agency. Consciousness and Cognition 17 (1), 219–239.

- Ticini, L.F., Schütz-Bosbach, S., Weiss, C., Casile, A., Waszak, F. When sounds become actions: higher-order representation of newly learnt action sounds in the human motor system. Journal of Cognitive Neuroscience, doi:10.1162/jocn_a_00134, in press.
- Tong, F., Nakayama, K., Vaughan, J.T., Kanwisher, N., 1998. Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21, 753–759.
- Von Holst, E., Mittelstaedt, H., 1950. Das Reafferenzprinzip. Naturwissenschaften 37, 464–476.
- Voss, M., Ingram, J.N., Haggard, P., Wolpert, D.M., 2006. Sensorimotor attenuation by central motor command signals in the absence of movement. Nature Neuroscience 9 (1), 26–27.
- Voss, M., Bays, P.M., Rothwell, J.C., Wolpert, D.M., 2007. An improvement in perception of self-generated tactile stimuli following theta-burst stimulation of primary motor cortex. Neuropsychologia 45 (12), 2712–2717.
- Vroomen, J., Stekelenburg, J.J., 2009. Visual anticipatory information modulates multisensory interactions of artificial audiovisual stimuli. Journal of Cognitive Neuroscience 22 (7), 1583–1596.
- Waszak, F., Herwig, A., 2007. Effect anticipation modulates deviance processing in the brain. Brain Research 1183, 74–82.
- Wegner, D.M., 2003. The mind's best trick: how we experience conscious will. Trends in Cognitive Science 7 (2), 65–69.
- Wolpert, D.M., 1997. Computational approaches to motor control. Trends in Cognitive Sciences 1 (6), 209–216.
- Wolpert, D.M., Ghahramani, Z., Jordan, M.I., 1995. An internal forward model for sensorimotor integration. Science 269, 1880–1882.
- Ziessler, M., Nattkemper, D., 2011. The temporal dynamics of effect anticipation in course of action planning. The Quarterly Journal of Experimental Psychology 64 (7), 1305–1326, doi:10.1080/17470218.2011.553067.