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Review article Precision control for a flexible body representation

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ABSTRACT

Adaptive body representation requires the continuous integration of multisensory inputs within a flexible 'body model' in the brain. The present review evaluates the idea that this flexibility is augmented by the contextual modulation of sensory processing 'top-down'; which can be described as precision control within predictive coding formulations of Bayesian inference. Specifically, I focus on the proposal that an attenuation of proprioception may facilitate the integration of conflicting visual and proprioceptive bodily cues. Firstly, I review empirical work suggesting that the processing of visual vs proprioceptive body position information can be contextualised 'top-down'; for instance, by adopting specific attentional task sets. Building up on this, I review research showing a similar contextualisation of visual vs proprioceptive information processing in the rubber hand illusion and in visuomotor adaptation. Together, the reviewed literature suggests that proprioception, despite its indisputable importance for body perception and action control, can be attenuated top-down (through precision control) to facilitate the contextual adaptation of the brain's body model to novel visual feedback.

1. Introduction

Many neuroscientists, psychologists, and philosophers believe that embodied selfhood, the experience of having a body and being in control of its actions, relies on some representation of the 'own' body in the brain (Damasio and Dolan, 1999; Graziano and Botvinick, 1999; Metzinger, 2004; Gallagher, 2006; Jeannerod, 2006; Makin et al., 2008; Gallese and Sinigaglia, 2010; Tsakiris, 2010; Proske and Gandevia, 2018; Riva, 2018; Hafner et al., 2020; Morasso and Mohan, 2021). Maintaining an adaptive neuronal body representation is a far from trivial task: On the one hand, it has to be stable enough for self-identification and action planning. On the other hand, it also has to be flexible enough to adapt to a constantly changing environment-and a constantly changing body. The latter kind of change can be caused by development or aging (Cowie et al., 2016; Gilmore and Johnson, 1997; Huxhold et al., 2006; Slaughter and Brownell, 2011), illness or accidents (Bard et al., 1995; Guedon et al., 1998); tool use (Heuer and Rapp, 2012; Liesner and Kunde, 2020; Maravita and Iriki, 2004; Miller et al., 2017, 2018), or, arguably, by immersion into virtual bodies (De Sanctis et al., 2013; Gonzalez-Franco et al., 2020; Lenggenhager et al., 2007; Sanchez-Vives and Slater, 2005; Vasser and Aru, 2020).

Recent theoretical work appealing to probabilistic Bayesian inference, particularly the framework of predictive coding (Rao and Ballard,

1999; Friston and Kiebel, 2009), has provided a new perspective on the mechanisms underlying body representation (Apps and Tsakiris, 2014; Allen and Friston, 2018; Hohwy, 2013; Seth et al., 2012; Seth and Tsakiris, 2018; Ciria et al., 2021; Limanowski and Blankenburg, 2013; Crucianelli et al., 2019). A key tenet of these proposals is that body representation in the brain can be described in terms of a hierarchical generative model, a hierarchy of probabilistic representations that models (or "predicts") the hidden causes of bodily sensations. Its parameters and structure can be updated by inverting the model; and integrating information from all relevant sensory modalities via probabilistic inference that can be described as approximately Bayesian. In other words, predictive coding approaches see the brain's 'body model' as a result of consolidating prior beliefs about the body with sensory evidence. This process may require fundamental decisions such as whether or not two sensory signals are believed to have originated from the same source--one's body (cf. Bayesian causal inference, e.g. Knill and Richards, 1996; Körding et al., 2007; Meijer and Noppeney, 2020).

An important concept within predictive coding approaches is that the relative impact of sensory evidence on these decisions—and potential ensuing body model updates—can be regulated. This is thought to be enabled by *precision control*; i.e., through adjusting prior beliefs about sensory precision. Changes in these beliefs determine how much weight should be assigned to sensory evidence from different modalities. This

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allows the brain to 'contextualise' sensory information processing and, thus, to bias inference; which can be helpful, for example, to focus on a task relevant modality while ignoring (salient) distractors (e.g., Gaspelin and Luck, 2018; Moorselaar and Slagter, 2020). Box 1 describes the

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concept of precision control in more detail; and how it can be linked to mental processes (i.e., attention) on the one hand, and to information processing in the brain (i.e., neuronal gain control) on the other.

An interesting implication of this idea is that predicted sensory

Box 1

Precision control, attention, and neuronal gain in perceptual inference.

Perceptual decision making can be described as a process of Bayesian inference; i.e., as inversion of a generative model, a hierarchy of probabilistic representations or 'beliefs', to infer how sensations were generated (Friston, 2005; Körding and Wolpert, 2006; Yon and Frith, 2021). Accordingly, the model's beliefs can be optimised by incorporating novel sensory evidence. This optimisation benefits from encoding the uncertainty in the respective sensory information; for instance, by representing it by a Gaussian probability density function (Knill and Pouget, 2004; Shadmehr et al., 2010; Ma, 2012). The variance of such a distribution represents (inversely) the estimated *precision* of the sensory inputs; which is naturally related to the amount of noise present in the sensory inputs. In the brain, this may be encoded through neuronal (population-level) variability; e.g., as "probabilistic population codes" (Ma et al., 2006).

Psychophysical experiments have shown that Bayesian inference can be applied to describe multisensory integration; i.e., the combination of sensory cues, weighted by their relative precision (Knill and Richards, 1996; Aitchison et al., 2021; Aitchison and Lengyel, 2017; Beauchamp, 2010; Ernst and Banks, 2002; van Beers et al., 1999; Rohe and Noppeney, 2015a,b, 2018; Meijer and Noppeney, 2020; Chancel et al., 2021). For instance, in spatial tasks related to body position estimation, vision is usually less variable—more precise—than proprioception, which may explain why it tends to 'dominate' proprioceptive cues under conflict (e.g., Botvinick and Cohen, 1998; van Beers et al., 1999, 2002).

Crucially, however, the weights assigned to sensory cues are not only determined by the variability of the information in each modality, but may also be changed 'top-down'. In other words, the above inferential process can be systematically biased by altering the relative influence of sensory cues on a multisensory representation; this may depend on cognitive variables such as, for example, a specific task set (Section 2.2). Such top-down modulation can be used, among other things, to compensate for inherent sensory noise of task-relevant stimuli; to enhance the processing of a task-relevant modality (e.g., vision in most visuospatial tasks); or to suppress the processing of salient but task-irrelevant stimuli. Likewise, it can be used to bias perceptual inference in scenarios where sensory estimates from multiple modalities conflict—e.g., to reduce uncertainty about body position, as focused in the present review.

One of the earliest, and to date most prominently proposed examples of top-down modulation of sensory processing is endogenous *attention* (Canon, 1970; Kelso et al., 1975). Indeed, as reviewed in Section 2.2, psychophysical studies have shown that attenting to a certain sensory modality increases its precision (Rohe and Noppeney, 2015a,b; Odegaard et al., 2016; Badde et al., 2020); brain imaging and electrophysiological studies have furthermore linked this to amplified sensory processing in the brain (e.g., Martinez-Trujillo and Treue, 2004; Talsma et al., 2007; Pestilli et al., 2011; Mima et al., 1998; Somers et al., 1999; Steinmetz et al., 2000).

The idea of a top-down modulation of sensory processing is a classical one; among others, it resonates with ideomotor theories (Greenwald, 1972; Hommel et al., 2001; Brass and Muhle-Karbe, 2014; Liesner and Kunde, 2020) and perceptual control theory (Powers, 1973; Jorgensen, 2020; Parker et al., 2020; George, 2008). The key challenge of this idea is the identification of the respective mechanisms and their implementation in the brain.

A popular framework that allows linking precision, attention, and neuronal processing is *predictive coding*. Recent formulations of predictive coding (Friston and Kiebel, 2009; cf. Rao and Ballard, 1999) postulate that the top-down modulation of sensory weights is achieved through changing higher-level beliefs about precision; which results in different predictions of precision assigned to the respective sensory inputs. Changing precision can be described as applying a multiplicative effect to bottom-up information flow; i.e., in- or decreasing precision estimates translates to augmenting or attenuating the impact of the respective sensory signals on inference or belief updating (Kok et al., 2012; Talsma, 2015; Parr and Friston, 2019). In folk-psychological terms, this can be described as attending or ignoring these sensations. The link between precision ad attention has been established by predictive coding based simulations of the Posner cueing paradigm (Feldman and Friston, 2010; cf. Posner, 1980); where simulated responses were faster at a stimulus location that was predicted to be more precise (i.e., the attended location), reproducing empirical behaviour. Other similar simulations were able to reproduce the phenomenon of psychophysical sensory attenuation in a force-matching task through attenuating sensory precision (Brown et al., 2013).

Within the predictive coding framework, different computational functions are assigned to neuronal populations in different cortical layers (e.g., following assumptions about the classical "canonical microcircuit", Bastos et al., 2012; Wang, 2010). Thus, predictive coding makes quite specific neurocomputational assumptions about how precision (i.e., attention) relates to *neuronal gain*, the multiplicative modulation of neuronal responsivity. In the brain, top-down modulations, specifically those linked to attention, are associated with increased blood flow and electrical activity in the cortical areas processing the respective stimulus (Posner and Dehaene, 1994; Desimone and Duncan, 1995; Dugué et al., 2020; Noonan et al., 2018; Gilbert and Sigman, 2007; Knudsen, 2007). Seminal electrophysiological studies have shown that this may be explained by a selective modulation of the responsivity of neuronal populations in those areas; i.e., of neuronal gain (Fries, 2001; Martinez-Trujillo and Treue, 2004; Pestilli et al., 2011). Building up on this, predictive coding proposes that precision control is implemented by altering the synaptic gain of specific neurons tuned to the respective stimulus; usually considered to be pyramidal cells in superficial cortical layers (Bastos et al., 2012; Heilbron and Chait, 2018).

A change in synaptic gain effectively scales the impact of the respective neuronal populations on their targets; in other words, gain control changes the input-output relationship of sensory areas, which affects within-area activity and between-area connectivity (cf. Fig. 1 for an example). This assumption has been corroborated by computational modelling of empirical brain responses using dynamic causal modelling (DCM; Friston et al., 2003), a framework that allows to formulate detailed models of intra- and inter-area neuronal message passing. Thus, attentional effects in the Posner cueing paradigm (which Feldman and Friston, 2010 had already linked to precision) could be associated with increased neuronal gain in visual areas (Brown and Friston, 2013). Similarly, an attentional enhancement of auditory prediction errors could be modelled in terms of increased neuronal gain in auditory cortices (Auksztulewicz and Friston, 2015). In sum, within predictive coding formulations, "precision control" means the contextual adjustment of sensory precision estimates based on prior beliefs, which can be linked to both attention and neuronal gain control.

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precision may not only be increased (e.g., by attention), but that it can also be *lowered*. This results in an attenuation of sensory information conveyed via the respective modality, and a correspondingly attenuated impact on higher-level inference (Brown et al., 2013). In the context of body representation, sensory attenuation seems somewhat paradoxical, as it implies a 'deliberate' suppression of information that, in principle, could have been used to update the body model. This review focuses on one particularly curious case of sensory attenuation; namely, as applied to proprioception during visuo-proprioceptive conflicts.

Proprioception (felt body position) and vision (seen body position) are arguably the most important senses for an action-oriented body representation. Proprioception in particular is indisputably fundamental for limb position perception and action control, and can be considered the 'default' sense for body representation (cf. Sakamoto et al., 1989; Pavlides et al., 1993; Ogawa and Imamizu, 2013; Proske and Gandevia, 2012; Vidoni et al., 2010; Salomon et al., 2013; Landelle et al., 2021; Prochazka, 2021). Thus, there are many cases in which humans rely on proprioception rather than some other (e.g., visual) bodily information; for instance, if a seen hand position differs too much from the felt one in terms of spatial distance or anatomical position, it is not self-attributed (Lloyd, 2007; Ide, 2013; Kalckert and Ehrsson, 2014; Kalckert et al., 2019).

In principle, however, the integration of both modalities has great behavioural benefits, as it improves body position estimates and offers some protection against a possible failure or miscalibration of either single modality (Ghahramani et al., 1997; Sober and Sabes, 2005; Ackerley et al., 2019; Lanillos and Cheng, 2018). Research over the past decades has made it clear that, within certain limits, humans can relatively easily adapt to visuo-proprioceptive conflicts; i.e., they can integrate the individual sensory estimates into a multisensory one and, potentially, recalibrate the individual estimates towards it (Fig. 1C; cf. Ghahramani et al., 1997; van Beers et al., 1999; Rossi et al., 2021).

The fact that mismatching visual input is tolerated by the body model at all points to a strong "natural prior" (Ma, 2012) about the unity of one's visuo-proprioceptive body representation; which is likely based on the life-long association of seen and felt hand positions, within certain anatomical limits (Limanowski and Blankenburg, 2013; Apps and Tsakiris, 2014). In other words, it seems that (within certain limits) the brain will combine deviant visual cues with proprioceptive ones, because it strongly believes that a common cause—one's body—has generated them.

Several scientists have speculated that a "distortion" or "suppression" of proprioception could help with this process: This argument has been made in two distinct, traditional lines of research on visuoproprioceptive conflicts: the "rubber hand illusion" (RHI, see Section 2.2; cf. Botvinick and Cohen, 1998; Apps and Tsakiris, 2014; Zeller et al., 2015; Limanowski and Blankenburg, 2016a,b; Crucianelli et al., 2019) and visuomotor adaptation (see Section 2.4; cf. Harris, 1963; Bernier et al., 2009).

The present review builds upon the idea that the above proposals can be described in terms of a contextual processing of visual vs proprioceptive body information in the brain, enabled by top-down precision control. Specifically, the attenuation of proprioceptive precision may help to (temporarily) prioritise vision over proprioception and, thus, to integrate both modalities under visuo-proprioceptive conflicts. Given the assumptions of predictive coding about the relationship between precision and neuronal gain, this should manifest itself as changes in the activity profiles of the respective sensory areas, and altered connectivity of these areas to multisensory areas (resulting from changes in the neuronal gain of sensory areas, cf. Box 1). Fig. 1 schematically shows the hypothesized changes in perceptual inference and their potential relation to cortical information processing.

In support of this idea, I shall review empirical evidence showing that humans can flexibly modulate proprioceptive (vs visual) gain within their brain's body model in a 'top-down' way; i.e., based on cognitive-attentional factors (Section 2.2; cf. Fig. 1B). Building up on

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this, I shall provide an overview of empirical data from the RHI and visuomotor adaptation (Sections 2.3 and 2.4; cf. Fig. 1C-D). I shall argue that the reviewed behavioural and neuronal correlates, together with the effects of brain stimulation, in each of the above three cases show that proprioceptive attenuation can help adapt the body representation to new sensory mappings; by allowing (novel or conflicting) visual information to be prioritized relative to proprioception. I shall conclude that proprioceptive attenuation, depending on contextual factors such as cognitive-attentional task sets, can be explained in terms of top-down precision control within the neuronal body model.

2. Contextual processing of visual vs proprioceptive body information

2.1. Selection of reviewed literature

The reviewed studies were selected based on pubmed and Google scholar searches with search terms related to the processing of conflicting visual vs proprioceptive information in general, as well as search terms related to each section's subtopic ("visuo-proprioceptive conflict (or recalibration)"; "visuomotor conflict (or recalibration)"; "attentional set"; "intersensory attention", "visual (or proprioceptive) attention"; "rubber hand illusion"; "body ownership"; and "visuomotor adaptation"). These search results were complemented by further references from recent relevant reviews (e.g., on the RHI: Grivaz et al., 2017; Salvato et al., 2019; Seghezzi et al., 2019; on sensorimotor learning: Hardwick et al., 2013; Ostry and Gribble, 2016; Rossi et al., 2021). This initial selection was narrowed down as follows.

Since the focus of this review was on the mechanism of precision control and its relation to the gain of visual vs proprioceptive cortical processing (Box 1), I focused on studies that measured cortical activity or interfered with it. A body representation that is ultimately aimed at the control of action must, of course, include a complex network of brain areas; including prefrontal, fronto-parietal (Desmurget et al., 1999; Contreras-Vidal and Kerick, 2004; Grafton et al., 2008; Krakauer et al., 2004; Lee and van Donkelaar, 2006; Mutha et al., 2011; Wolpert et al., 1998), and subcortical structures (e.g., the cerebellum and the basal ganglia, cf. Doyon et al., 2009; Seidler et al., 2006; Tanaka et al., 2009; Tseng et al., 2007; Tzvi et al., 2020). However, the effects of top-down precision control should manifest themselves in terms of changes in neuronal activity in the respective cortical sensory area targeted by this modulation (Fig. 1). This means that, for this review, the regions of primary interest were the sensory cortices that process visual or proprioceptive body information; i.e., the primary and secondary visual (V1, V5, and lateral occipitotemporal cortex, LOC) and somatosensory (S1, S2) or motor (M1) cortices. However, given that most of the scenarios reviewed in the following involved visuo-proprioceptive conflicts, we should also expect an involvement of fronto-parietal (i.e., premotor and posterior parietal) cortices, because they are known hubs for integration of visual and proprioceptive body information (Sakata et al., 1973; Rushworth et al., 1997; Graziano et al., 2000; Graziano, 1999; Avillac et al., 2007).

This included studies measuring somatosensory evoked potentials (SEPs), as these originate from the S1 (Allison et al., 1989; Longo et al., 2011; Wood et al., 1985). It also included studies measuring motor evoked potentials (MEPs) recorded from the periphery after stimulation of M1, as these measures likely reflect attenuation of activity in the (sensori-) motor cortex (della Gatta et al., 2016; Isayama et al., 2019).

Brain *stimulation* studies that targeted cortical areas were also included in this review; i.e., experiments in which a certain brain area was artificially stimulated or disturbed. From a predictive coding perspective, this can be described as directly manipulating 'bottom-up' sensory precision. Note that these studies cannot tell us anything about top-down precision control per se. However, they can show that changing sensory precision via brain stimulation has the same behavioural effects as changing it via top-down precision control in the same

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Fig. 1. How precision control could help adapt the body representation to conflicting visual input. This schematic example shows a hypothetical sequence of Bayesian inference about one's hand position given visual (V) and proprioceptive (P) bodily cues (top row; showing Gaussian probability density functions); the associated changes in cortical information processing as derived from predictive coding (middle row; here assuming information flowing from primary and/or secondary visual and proprioceptive areas to multisensory posterior parietal areas); and the possible associated changes in the perception of the own body (bottom row). For details, see Box 1. A: In this example, visuo-proprioceptive conflict is present (e.g., experimentally introduced through displacing vision of the hand). Under the assumption of a common cause (based on a strong prior belief in visuo-proprioceptive congruence, see main text), this poses a problem for the brain's body model, because the sensory cues convey different information about hand position. In principle, the brain could still combine both estimates into a multisensory estimate-but the confidence in this estimate might not be very high. Given a large enough discrepancy, a common cause for V and P may not be inferred at all (and vision will be discarded in favour of proprioception, see main text). B: To resolve this kind of uncertainty about one's hand position, precision control can be used to bias inference. The precision of the sensory cues (corresponding to the inverse variance-the width-of the respective Gaussian probability density function) is predicted by a hierarchically higher prior belief (cf. Box 1), which itself can be adjusted: Here, the predicted precision of V is increased (corresponding to decreasing the variance of the probability density function) and that of P is attenuated. This can be described as applying a multiplicative gain to bottom-up information flow within the cortical hierarchy (Box 1). Thus, changing the predicted precision of two sensory signals V and P corresponds to modulating the gain of brain areas V and P; i.e., the sensitivity of these neuronal populations to their respective sensory inputs. One would expect this to be linked to changes in brain activity (reflected by the thickness of the circles' borders) on the one hand, and changes in brain connectivity (reflected by the thickness of the arrows) on the other: The sensory input received by region V is predicted to be more precise, therefore region V's gain is increased and information routed via V to hierarchically higher regions is emphasized; conversely, information routed via P is attenuated by reducing P's gain. The sources of these modulations are not shown here; they could be in prefrontal, posterior parietal, or even subcortical structures. Finally, the above processes may correspond to a perceptual and psychophysical attenuation of the felt hand relative to the seen one (observable, for example, as increased uncertainty about position or impaired somatosensory processing, see Sections 2.3 and 2.4 for examples). C: Adjusting precision can influence the integration of both cues into a multisensory estimate VP, which will now be clearly biased toward the more precise cue V. It may also affect the degree of sensory recalibration; i.e., the-attenuated-proprioceptive hand position towards the visual, or the inferred multisensory one (indicated by the pink arrow, see main text for details). The associated perception may be that of a new, 'unified' hand position, closer to the dominant (more precise) visual cue. D: Potentially, precision control may only be temporarily required; i.e., to reduce uncertainty about one's body representation given a novel, unpredicted multisensory mapping. Once the prior belief about hand position has been updated (i.e., a new hand position has been confidently inferred), precision and cortical processing could return to their previous state.

experimental paradigm. Thus, brain stimulation studies can supplement the interpretation of the results of the reviewed brain imaging studies in terms of top-down precision control. Some of these studies provided MNI coordinates for the targeted brain area (Tsakiris et al., 2008; Wold et al., 2014). For studies providing targeted locations in terms of EEG cap electrodes (Hornburger et al., 2019; Kammers et al., 2009a), the anatomical locations displayed in Fig. 3D have been approximated following Herwig et al. (2003) and Towle et al. (1993). Stimulation studies targeting the primary motor (M1) or somatosensory (S1) cortex have focused on the location of the respective hand area (i.e., the "motor hotspot" or an area 2.5–3 cm behind it, cf. Balslev, 2004; della Gatta et al., 2016; Isayama et al., 2019; Yoon et al., 2014), which has therefore been schematically indicated in Figs. 3D and 4D.

Table 1 lists the experimental studies and meta-analyses used to generate the neuroanatomical overviews in Figs. 2–4, using the SPM12 (Wellcome Trust Centre for Neuroimaging, University College London, https://www.fil.ion.ucl.ac.uk/spm/) brain template. Please note that the graphical overviews are simply intended to schematically illustrate the cortical locations of activations or deactivations. Since the reviewed studies almost exclusively examined right-handed participants, the

neuronal correlates (particularly in the somatomotor cortex) were predominantly localised to the left brain hemisphere. Figs. 2–4 therefore show a left hemisphere render, with effects localized to the right hemisphere indicated with dotted outlines (see figure legends for details). Any reported subcortical activations in the brain imaging studies included in Figs. 2–4 are listed in Table 1; results that were not source localized, or for which no coordinates were reported, are discussed in the main body of the text.

2.2. Visual vs proprioceptive processing depending on attentional set

Within predictive coding accounts of brain function, the top-down modulation of sensory (prediction error) information through changing their associated precision is closely linked to the concept of *attention* (Box 1). This resonates with the classical association between the top-down modulation of sensory processing and attention (Folk et al., 1992; Eimer and Kiss, 2008; Gilbert and Sigman, 2007; Knudsen, 2007; Parr and Friston, 2019; Talsma et al., 2010; Tang et al., 2016; although there are other relatable concepts such as expectation, cf. Richter et al., 2018; Alink and Blank, 2021; Summerfield and Egner, 2009; Yon et al.,

Table 1

Details of studies and meta-analyses included in Figs. 2–4. See the respective Sections of the main text for details.

Visual > propriocept	ive attentional set (Fig. 2B, S	ection 2.2)							
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Grefkes et al. (2004)	fMRI (BOLD)	Movement with/without visual feedback (cursor/joystick)	Right	Use visual > proprioceptive feedback	Fig. 4	-			
Limanowski and Friston (2020a)	fMRI (BOLD)	Phase matching under visuo- proprioceptive conflict (virtual hand/ glove)	Right	Use visual > proprioceptive feedback	Table 1, Figs. 2a & S11	-			
Limanowski et al. (2020)	MEG (SSR)	Phase matching under visuo- proprioceptive conflict (virtual hand/ glove)	Right	Use visual > proprioceptive feedback	Fig. 2	-			
Proprioceptive > visi	ual attentional set (Fig. 2C, S	ection 2.2)							
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Grefkes et al. (2004)	fMRI (BOLD)	Movement with/without visual feedback (cursor/joystick)	Right	Use proprioceptive > visual feedback	Fig. 5	-			
Limanowski and Friston (2020a)	fMRI (BOLD)	Phase matching under visuo- proprioceptive conflict (virtual hand/ glove)	Right	Use proprioceptive > visual feedback	Table 1, Fig. 2a	-			
Rubber hand illusion	: cortical correlates (Fig. 3B,	Section 2.3.1)							
Reference	Method			Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Salvato et al. (2019)	Meta-analysis (multilevel ker	nel density analysis)		"Body ownership"	Table 1, Fig. 1	L/R cerebellum			
Seghezzi et al. (2019)	Meta-analysis (activation like	lihood estimation)		"Body ownership"	Table 2, Fig. 3	-			
Grivaz et al. (2017) Rubber hand illusion	Peak activation overview of studies on: attenuation (Fig. 3C, Section 2.3.2)			"Body ownership"	Fig. 1a	-			
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
della Gatta et al. (2016)	TMS/EMG: L. M1 (MEP)	Synchronous vs asynchronous visuo- tactile stimulation vs baseline	Right	Synchronous < asynchronous stroking	Fig. 3	-			
Isayama et al. (2019)	TMS/EMG: L. M1,S1,PPC (MEP,SAI,LAI,PD)	Synchronous vs asynchronous visuo- tactile stimulation vs baseline	Right	Synchronous < baseline	Table 1, Fig.				
Limanowski and Blankenburg (2016b)	fMRI (BOLD)	Synchronous vs asynchronous visuo- tactile stimulation vs real hand stimulation only	Bilateral	Synchronous < asynchronous & synchronous < real hand	Table 2, Fig. 3b	_			
Tsakiris et al. (2007)	PET (rCBF)	Synchronous vs asynchronous visuo- tactile stimulation/congruent vs incongruent rubber hand identity	Right	Conflict interaction effect	Table 1	_			
Zeller et al. (2015)	EEG (EP)	Visuo-tactile stimulation of congruently vs incongruently placed real and rubber hand vs real hand stimulation only	Bilateral	Congruent < incongruent & congruent < real hand (right hand side)	Table 1, Figs. 3 and 4	-			
Rubber hand illusion: brain stimulation (Fig. 3D. Section 2.3.1/2)									
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Fossataro et al. (2018)	rTMS: L. M1 (illusion score, proprioceptive drift)	Synchronous vs asynchronous visuo- tactile stimulation	Right	Synchronous > asynchronous stroking (rTMS > sham)	Fig. 2	-			
Frey et al. (2020)	iTBS: R. S1 (illusion score, proprioceptive drift)	Synchronous visuo-tactile stimulation	Left	iTBS < sham TBS	Fig. 5	-			
Hornburger et al. (2019)	tDCS: L. S1 (illusion score)	Synchronous vs asynchronous visuo- tactile stimulation	Right	Synchronous > asynchronous stroking (Cathodal > anodal tDCS)	Table 1, Fig. 2	-			
Kammers et al. (2009a)	rTMS: L. IPL (proprioceptive drift, illusion score, reaching)	Synchronous vs asynchronous visuo- tactile stimulation	Right	Synchronous < asynchronous stroking (rTMS > sham)	Fig. 2	_			
Tsakiris et al. (2008)	rTMS: R. TPJ/IPL (proprioceptive drift)	Synchronous visuo-tactile stimulation of rubber hand vs object	Left	Rubber hand < object (rTMS, over TPJ > over vertex)	Fig. 2	-			
Wold et al. (2014)	rTMS: L. LOC (illusion score, proprioceptive drift)	Synchronous vs asynchronous visuo- tactile stimulation	Right	Synchronous > asynchronous stroking (rTMS > sham)	Fig. 2	_			

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Table 1 (continued)

visuomotor adaptati	on: cortical correlates, early	> fate (Fig. 4b, Section 2.4.1)							
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Anguera et al. (2007)	fMRI (BOLD)	Pointing with rotated vision (cursor/ joystick)	Right	Early adaptation (decaying exponential function; and early > unrotated)	Table 3, Fig. 6	-			
Anguera et al. (2010)	fMRI (BOLD)	Pointing with rotated vision (cursor/ joystick)	Right	Early $>$ late adaptation	Table 5a	-			
Graydon et al. (2005)	fMRI (BOLD)	Pointing with rotated vision (cursor/ joystick)	Right	Learning-related decrease	Table 2	-			
Inoue et al. (1997)	PET (rCBF)	Pointing with rotated vision (video/ finger)	Right	Early $>$ late & early $>$ reach	Table 2	-			
Limanowski et al. (2017)	fMRI (BOLD)	Hand-target pursuit tracking under varying visual delay (virtual hand model/data glove)	Right	Early response to visuomotor mapping change	Table 1, Fig. 4b	-			
Luauté et al. (2009)	fMRI (BOLD)	Pointing with reversed vision (prisms/ finger)	Right	Early $>$ late adaptation	Table 2, Fig. 3	R cerebellum			
Seidler et al. (2006)	fMRI (BOLD)	Pointing with rotated vision (cursor/ joystick)	Right	Early > late adaptation	Table 1, Fig. 4	L/R basal ganglia, R cerebellum			
Tzvi et al. (2020)	fMRI (BOLD)	Pointing with rotated vision (cursor/ mouse)	Right	Early > late (linear decrease in adaptation)	Table 2, Fig. 3	L cerebellum, vermis			
Visuomotor adaptati	on: attenuation (Fig. 4C, Sect	tion 2.4.2)							
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Bernier et al. (2009)	EEG (SEP)	Tracing with reversed vision (pen/ mirror)	Right	Early < normal trials	Fig. 3	-			
Inoue et al. (1997)	PET (rCBF)	Pointing with rotated vision (video/ finger)	Right	Early < late (& late > reach)	Table 3	-			
Inoue et al. (2000)	PET (rCBF)	Pointing with rotated vision (video/ finger)	Right	Early < late (& late > reach & late > saccade)	Table 3, Fig. 5	-			
Visuomotor adaptation: brain stimulation (Fig. 4D, Section 2.4.2)									
Reference	Modality (Measures)	Task	Hand side	Effect of interest	Original Figure or Table	Subcortical/ cerebellar activations			
Balslev (2004)	rTMS: L. S1 (error)	Tracing with reversed vision (cursor/ mouse)	Right	Error (% baseline) in early trials (rTMS < sham)	Fig. 3	-			
Yoon et al. (2014)	rTMS: L. S1 (proprioceptive shift)	Pointing with reversed vision (prisms/ finger)	Right	Shift rTMS > sham (terminal visual feedback)	Table 1, Fig. 3	-			

BOLD = blood oxygenation level dependent signal, EEG = electroencephalography, EMG = electromyography, fMRI = functional magnetic resonance imaging, iTBS = intermittend theta burst stimulation, MEG = magnetoencephalography, MEP = motor evoked potentials, PD = proprioceptive drift, PET = positron emission to-mography, rCBF = regional cerebral blood flow, SAI/LAI = Short-/long-latency afferent inhibition, (S)EP = (somatosensory) evoked potentials, SSR = steady state responses, tDCS = transcranial direct current stimulation, (r)TMS = (repetitive) transcranial magnetic stimulation.

2018). A discussion of the nature of attention is beyond the scope of this review; here, it shall loosely be defined in the folk-psychological sense, as an allocation of (overall limited) resources to stimulus processing.

Unisensory tasks have established that attention to the sensory stimuli can modulate brain activity in the respective sensory cortices; including visual (Martinez-Trujillo and Treue, 2004; Pestilli et al., 2011; cf. Kastner and Ungerleider, 2000; Treue, 2001; Carrasco, 2011 for reviews) and somatosensory (Mima et al., 1998; Somers et al., 1999; Steinmetz et al., 2000; Fujiwara et al., 2002; Bauer et al., 2006; Dockstader et al., 2010; Gomez-Ramirez et al., 2016; Wiesman and Wilson, 2020) cortices. For this review, the important form of attentional control is in the context of visuo-proprioceptive conflict; where selective attention to one modality can be used to prioritize the processing of the respective stimuli over those received from another modality (sometimes also referred to as "crossmodal" or "intersensory" attention, cf. Driver, 2001; Rowe et al., 2002; Macaluso and Driver, 2005). For instance, previous work has shown that attention can modulate the neuronal responses of cortices processing the respective attended, relative to the unattended modality when visual and auditory stimuli (Alho et al., 1994; Foxe and Simpson, 2005; Auksztulewicz et al., 2017a,b) or auditory and tactile stimuli (Hötting et al., 2003) are presented simultaneously. Similarly, the responses of visual and somatosensory cortices to simultaneously presented visual and tactile stimuli can be modulated by attention, in a way consistent with an attentional prioritization of task-relevant information (Bauer et al., 2012; cf. Foxe and Snyder, 2011 for a review). These modulations can influence multisensory

integration: When integrating conflicting visual and auditory information under the assumption of a common cause, modality-specific attention changes the neural and behavioural weights assigned to the attended modality, and thus influences its relative impact on the multisensory estimate (Rohe and Noppeney, 2015a,b, 2018; cf. van Beers et al., 1999; Ernst and Banks, 2002). Together, these findings provide support for the classical idea of attentional 'sets'; i.e., the adoption of a specific contextual processing mode, in which some sensory information is prioritized over another (Gibson, 1941; cf. Posner et al., 1978; Folk et al., 1992; Kelso et al., 1975; Redding et al., 1985; cf. Eimer and Kiss, 2008; Lien et al., 2010; González-García et al., 2020).

So, can one change one's attentional set to alter the processing of *proprioceptive vs visual* body information? Classical behavioural work has shown that in experimental settings with conflicting visual and proprioceptive body position information, participants have a tendency to attend to vision 'per default' (Canon, 1970; cf. Hay et al., 1965; Kelso, 1979; Klein and Posner, 1974; Posner et al., 1976; Redding et al., 1985). However, Kelso et al. (1975; cf. Posner et al., 1978) demonstrated that people can counteract this bias; i.e., they can increase attention to proprioception—which changes the variability of the perceived own limb position, and the degree of proprioceptive recalibration (a shift of the perceived own limb position towards the displaced visual limb position). Based on the tight link between attention, precision and neuronal gain postulated by predictive coding (Box 1), one would expect these changes to be associated with altered activity in visual and proprioceptive brain areas (cf. Fig. 1).

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Indeed, there is some evidence for corresponding changes in visuoproprioceptive tasks; e.g., due to the adoption of a specific attentional set. In an fMRI study, Grefkes et al. (2004) had their participants move a cursor to a target via a joystick, while providing visual feedback or not. The availability of visual feedback effectively changed the modality used for action guidance (i.e., vision or proprioception), which was reflected in diametrical activity changes in visual and somatomotor cortices (Fig. 2B vs C). Given the strong link between hemodynamic activity, neuronal gain, and attention (see above), this suggests that participants increased the gain (precision) of vision when it was available, and proprioception when vision was unavailable.

In our own recent work, we have developed a virtual reality based phase matching task, designed to induce a visual or proprioceptive attentional set (Fig. 2A; cf. Limanowski et al., 2020; Limanowski and Friston, 2020a,b). In this design, the participant controlled a photorealistic virtual hand model via a data glove worn on the unseen hand. The task consisted of matching an oscillatory target pattern (a shrinking-and-growing fixation dot) with recurrent grasping movements; either with the real unseen hand or with the seen virtual hand. Crucially, the design contained an experimental factor 'visuo-proprioceptive congruence'; i.e., half of the time, the movements of the virtual hand were displaced (temporally delayed) with respect to the actually executed movements. This manipulation increased task difficulty, as now only one of the modalities (seen or felt hand) could be matched to the target phase, while the other one was per design out of phase. Effectively, phase matching vision under incongruence required a focus on vision and a realignment of one's executed movements (proprioception). Conversely, matching proprioception under incongruence required ignoring a conflicting visual movement. This turned out to be challenging for most participants-which can be explained by the fact that incongruent observed movements tend to strongly bias one's own executed movements (Blakemore and Frith, 2005; Brass et al., 2001; Garbarini et al., 2013; Kilner et al., 2003; Press et al., 2011).

In brief, and as evident from the participants' self-reports (Fig. 2A), the task instructions seemed to create an attentional 'set' in which participants focused on the instructed sensory modality. Using fMRI, we (Limanowski and Friston, 2020a) could show diametrical cortical activity changes: a visual set was associated with significantly increased activity in posterior parietal and (applying small-volume correction) visual areas; a proprioceptive set was associated with increased activity the secondary somatosensory cortex (S2, contralateral to the moving

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hand). We subjected these hemodynamic changes to a network analysis using dynamic causal modelling (DCM, Friston et al., 2003), a method with which the effects of changes in neuronal activity on a measured variable (such as the BOLD signal) are mathematically modelled (cf. Box 1). This revealed that, in the brain network processing visuo-proprioceptive bodily action feedback, visual vs proprioceptive attentional set was reflected by changes in the local gain of neuronal populations in the primary visual cortex (V1) and the S2: V1 gain was increased under a visual set, whereas S2 gain was increased under a proprioceptive set. Using an analogous task design in a magnetoencephalography (MEG) scanner, we (Limanowski et al., 2020) could further link those changes in neuronal gain to suppressed or increased (depending on set) oscillatory power in the beta (12-20 Hz) frequency range over visual areas. Suppression of low-frequency oscillations is thought to indicate attentional control in general (Engel and Fries, 2010; Bastos et al., 2015; Wang, 2010); and in particular, during intersensory conflicts (Foxe et al., 1998; Bauer et al., 2006, 2012; Lebar et al., 2015, 2017). Within predictive coding approaches, low-frequency power has been linked to predicted precision (Sedley et al., 2016; Palmer et al., 2016, 2019). Notably, in our study, changes in (modelled) neuronal gain were particularly strong under visuo-proprioceptive conflict; i.e., in scenarios where prioritizing one modality implied ignoring the other. Furthermore, as a conceptual 'proof of principle', we recreated this task design in a computational simulation based on the predictive coding framework (Limanowski and Friston, 2020b). In brief, we could show that a simulated agent performed the above task much better when it increased the precision of the sensory signals (i.e., prediction errors) from the respective instructed modality, and decreased those of the currently 'irrelevant' modality. The resulting simulated behaviour closely resembled that of human participants who attended the respective instructed modality while ignoring the other one.

Together, these findings support the general link between attention and cortical gain in terms of top-down precision control; and specifically, the idea that the processing of visual vs proprioceptive information about one's own moving body can be selectively regulated by precision control. This means that even proprioceptive information about the own body can, in principle, be attenuated. In the next two sections, we shall consider two examples, in which such a re-balancing of visual vs proprioceptive information—including the notable attenuation of proprioception—may be involved; i.e., the rubber hand illusion and visuo-motor adaptation.



Fig. 2. Visual vs proprioceptive cortical processing depending on attentional set. Specific experimental designs allow the comparison of the effects of attentional task sets on the processing of visual vs proprioceptive action feedback. **A:** For instance, the task relevance of vision vs proprioception can be manipulated in goal-directed movement tasks (reprinted with permission from Limanowski et al., 2020). Here, the participant has to follow an oscillatory target pattern with recurrent grasping movements; either with the unseen real hand or with a seen virtual hand model that she controls via a data glove. This seems to induce an attentional set in which participants prioritise one sensory modality over the other, which is particularly evident when a visuo-proprioceptive conflict is introduced (here, via visual delay). See Section 2.2 for details. **B:** Cortical activity associated with a prioritisation of vision over proprioception has been observed in the posterior parietal cortex (PPC) along the intraparietal sulcus (IPS), and in the visual cortex (LOC = lateral occipitotemporal cortex). CS = central sulcus. The anatomical locations (MNI coordinates) of the respective significant peak effects of each study are indicated with coloured circles; dashed lines indicate peaks in the right hemisphere. **C:** Cortical activity associated with a prioritisation of proprioception over vision has been observed in the contralateral sensorimotor cortex. See Table 1 for details.

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2.3. Static visuo-proprioceptive conflicts: the rubber hand illusion

The so-named 'rubber hand illusion' (RHI, Botvinick and Cohen, 1998) is one of the most prominent examples of experimentally investigating visuo-proprioceptive conflicts (for reviews, see Botvinick, 2004; Makin et al., 2008; Blanke et al., 2015; Kilteni et al., 2015; Grivaz et al., 2017; Salvato et al., 2019; Seghezzi et al., 2019; Ehrsson, 2020). In the RHI, the participant sees a fake hand at a different location than her real hand, which is hidden from view (Fig. 3A). So there is a conflict between visual and somatosensory (i.e., proprioceptive) information about hand position. Typically, the fake hand and the real hand are then touched congruently (with control conditions being asynchronous touch or touch at different anatomical locations). In most participants, this induces the experience of 'feeling' the touch on the fake hand, often accompanied by a self-attribution of the fake hand—as evident from self-reports and various behavioural measures.

The most prominent behavioural measure of the RHI is the so-named proprioceptive drift: Following the induction of the RHI (compared with experimental control conditions), participants tend to perceive their own hand position closer towards the location of the (displaced) rubber hand (Botvinick and Cohen, 1998), which may also affect subsequent reaching movements with the real hand (Holmes et al., 2004; Zopf et al., 2011; Butz et al., 2014; Fang et al., 2019). This is reminiscent of the visual "capture" of proprioception as observed in many scenarios of hand localisation (cf. Tastevin, 1937; cf. Holmes et al., 2006; Kelso et al., 1975; Pavani et al., 2000; Posner et al., 1976; Yeh et al., 2017). I.e., the proprioceptive hand position is recalibrated towards the hand position conveyed by the 'dominant' visual modality (cf. Fuchs et al., 2016; Hinz et al., 2018; Körding et al., 2007; Schürmann et al., 2019). This can be explained in terms of Bayesian inference, taking into account the relatively higher sensory precision of vision (e.g., Armel and Ramachandran, 2003; Kilteni et al., 2015; Samad et al., 2015; Hinz et al., 2018; Fang et al., 2019; Fossataro et al., 2020; Rood et al., 2020; Chancel et al., 2021). As the RHI is a static design, this effect could be enhanced by the fact that proprioceptive signals about hand position decay within tens of seconds (Brown et al., 2003; Holmes et al., 2006; Wann and Ibrahim, 1992). In sum, the RHI seems to be related to a recalibration of proprioception as schematically indicated in Fig. 1C.

There is compelling evidence that the variables measured during the RHI reflect a general process of changing the visuo-proprioceptive body representation that applies to other body parts, and potentially even the full body (Petkova et al., 2011). Thereby the congruent touch is thought to be a mere amplification of the RHI. Analogous behavioural and neuronal correlates can be observed without visuo-tactile stimulation (Limanowski and Blankenburg, 2016a; Martinaud et al., 2017); much like it has been suggested by electrophysiological work in monkeys (Graziano et al., 2000; Graziano, 1999), and by experiments showing that the perception of hand position can be biased simply by using mirrors to displace vision (Holmes et al., 2004, 2006; Kammers et al., 2009b).

Botvinick and Cohen (1998) had already speculated that the RHI "relies upon a distortion of the position sense" (p. 756). More recently, it has been proposed that proprioceptive attenuation may be applied 'strategically' in the RHI, to augment the recalibration of proprioception towards vision; i.e., as a result of a higher-level process of inference that aims to keep the body representation unified in face of conflicting visuo-proprioceptive inputs (Zeller et al., 2015, 2016; Limanowski and Friston, 2018; Riva, 2018; Hornburger et al., 2019; Isayama et al., 2019; Crucianelli et al., 2019; cf. Kilteni et al., 2015). As described in Fig. 1, this could, in principle, be achieved through precision control; i.e., through a top-down attenuation of proprioceptive precision. Indeed, there is tentative evidence linking the strength of the RHI experience to general attentional flexibility (Yeh et al., 2017), which could support this idea.

Meanwhile, a substantial amount of behavioural, brain imaging, electrophysiological, and psychophysical data has been accumulated.

So, what empirical evidence is there that the brain actively regulates proprioceptive vs visual precision during the RHI?

2.3.1. Cortical correlates

Ehrsson et al. (2004) investigated the RHI for the first time inside an MR-scanner, leading the way for an extensive body of imaging end electrophysiological work providing insights into the neuroanatomy underlying the illusion. Three recent meta-analyses (Grivaz et al., 2017; Salvato et al., 2019; Seghezzi et al., 2019) have summarized brain activations reported by studies investigating 'body ownership' with the RHI, or slight variations of the paradigm. As shown in Fig. 3B (cf. Table 1), these analyses have identified overall consistent activations of the premotor (PMC, predominantly its ventral parts) and posterior parietal cortex (PPC, predominantly around the intraparietal sulcus, IPS), and of the visual lateral occipitotemporal cortex (LOC). While not reaching significance in the meta-analysis by Seghezzi et al. (2019), the premotor cortex (PMC) is strongly implied by the literature (cf. de Haan and Dijkerman, 2020; Ehrsson, 2020; Fang et al., 2019); likewise, while the LOC cluster did not reach significance in the statistical analysis of Grivaz et al. (2017), their peak activation overview of (cf. Fig. 3B) shows a substantial activation overlap within the LOC.

Moreover, activity in each of these areas (PMC, PPC, and LOC) has been found to correlate positively with proprioceptive drift and/or with reported (illusory) self-attribution of the fake hand (Ehrsson et al., 2004; Gentile et al., 2013; Limanowski et al., 2014; Limanowski and Blankenburg, 2015, 2016a; Tsakiris et al., 2007). *Electrophysiological studies* have furthermore reported increased gamma-band activity during the RHI (Kanayama et al., 2007, 2009), which, through intracranial recordings, could most strongly be associated with the PMC and PPC (Guterstam et al., 2019). Attenuated event-related potentials (Rao and Kayser, 2017) and power changes in the mu-band (Evans and Blanke, 2013) have also been found over the fronto-central electrodes (likely originating from the fronto-parietal cortex, potentially spanning across the sensorimotor cortex).

Together, the above findings clearly point to a functional role of the PMC, PPC, and LOC in the illusory 'adoption' of the fake hand. This aligns well with previous work implicating these areas in representing the upper limb for goal-directed action based on visual and proprioceptive information. The fronto-parietal reaching circuit has been thoroughly investigated in seminal electrophysiological work in monkeys, which have revealed neurons with multimodal receptive fields in the PPC and PMC; which encode the visual and proprioceptive upper limb position and, sometimes, their congruence (Sakata et al., 1973; Rushworth et al., 1997; Graziano et al., 2000; Graziano, 1999; Avillac et al., 2007). A whole-brain fMRI replication of these studies in humans identified the homologue areas in the PMC and PPC, and notably, also in the LOC (Limanowski and Blankenburg, 2016a). Recently, researchers have identified a region in the LOC, the extrastriate body area (EBA, cf. Downing et al., 2001), which exhibits a strong preference for visual body (action) feedback (cf. Astafiev et al., 2004; Lingnau and Downing, 2015; Makin et al., 2012). Using separate functional localization of visually body part selective brain areas, recent fMRI studies have demonstrated that RHI-related activations in the LOC fell within the EBA (Limanowski et al., 2014; Limanowski and Blankenburg, 2015, 2016a).

Brain connectivity and network analyses have further illuminated the respective roles of fronto-parietal and visual areas in the RHI: Functional connectivity analyses have revealed an illusion-related increased information exchange between the PMC, PPC, and LOC; alongside other areas in the visual cortex, supramarginal gyrus, and putative somatosensory cortex (Gentile et al., 2013; Limanowski and Blankenburg, 2015, 2016a). Thereby connectivity between the LOC and the PPC seems to increase particularly early (Limanowski and Blankenburg, 2017). The nature of these connectivity modulations has been further investigated using DCM. DCM on EEG (Zeller et al., 2016) and fMRI (Limanowski and Blankenburg, 2015) data has thus revealed that the connectivity modulations observed during the RHI are likely due to an increased

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'bottom-up' information flow from the LOC to the PPC. A similarly increased 'bottom-up' flow from the S1 (Guterstam et al., 2019) or S2 (Limanowski and Blankenburg, 2015) to the PPC has also been suggested. However, in variations of the RHI paradigm without visuo-tactile stimulation, only an enhanced LOC-PPC communication can be observed (Limanowski and Blankenburg, 2017). In contrast to somatosensory information flow, which has been interpreted to reflect the processing of 'embodied' touch (Guterstam et al., 2019; Shokur et al., 2013), the visual-to-parietal information flow thus likely reflects increased visual body information processing per se. Finally, using renormalized partial directed coherence on EEG data, Kanayama et al. (2017) have shown that the causal influence of medial frontal areas on the PPC inversely correlated with the strength of the RHI; potentially suggesting a relaxation of top-down constraints on multisensory integration in the PPC.

Brain stimulation studies (Fig. 3D; see Golaszewski et al., 2021 for a review) have largely supported the importance of the brain areas identified as contributing to the RHI in the above imaging studies; albeit not entirely consistently. Interference with activity in the left inferior parietal lobe (Kammers et al., 2009a; off-line repetitive transcranial magnetic stimulation, rTMS) and in the right temporo-parietal junction (Tsakiris et al., 2008; single-pulse TMS) was associated with relatively reduced strength of the RHI, as measured by proprioceptive drift (although ownership reports or reaching actions were unaffected). This supports the crucial role of the PPC in the RHI, presumably per the multisensory integration of conflicting visual and proprioceptive information. Inhibiting the right PMC via rTMS did not influence ownership illusion ratings, but the detection of visuo-tactile synchrony; this could hint towards a more indirect role of the PMC in the RHI (Peviani et al., 2018). In contrast to inhibition via rTMS, *stimulating* the right PMC and PPC with intermittent theta burst stimulation (iTBS) had no effect on the RHI (Mioli et al., 2018). The authors speculate that this could indicate a ceiling effect of illusory ownership, which cannot be further enhanced, or potentially also be due to methodological limitations of iTBS. Somewhat surprisingly, one study also reported that interference with activity in the LOC via rTMS was associated with increased proprioceptive drift (but no effect was observed on illusion scores or illusion onset time, Wold et al., 2014). One potential explanation, proposed by the authors, could be that a disruption of a visual own body image within the EBA might have facilitated the illusory incorporation of a different looking fake hand.

In sum, the above brain imaging and stimulation literature suggests that the RHI is associated with an enhanced processing of visual body information (i.e., of visual information about body position from the fake hand) and its integration with the multisensory body representation.

2.3.2. Proprioceptive attenuation

Conversely, as we shall see now, there is strong evidence for an attenuation of proprioceptive body information (i.e., of somatosensory information from the real hand) during the RHI. Firstly, behavioural studies have shown that the RHI is associated with an impaired processing of somatosensory information from the real hand; e.g., with slower detection of tactile stimuli (Folegatti et al., 2009) or heightened tactile discrimination thresholds (Moseley et al., 2008). Furthermore, participants with higher proprioceptive acuity have been found to be less susceptible to the RHI (Horváth et al., 2020; Pyasik et al., 2019). In contrast, proprioceptive deficits following right hemispheric stroke positively correlated with the strength of the RHI (Martinaud et al., 2017). Correspondingly, artificially 'removing' proprioception by a week-long limb immobilisation enhanced the RHI, as measured by proprioceptive drift and self-reports (Burin et al., 2017). Crucianelli et al. (2019) showed that intranasal oxytocin, which has been linked to the modulation of synaptic gain in a way that promotes somatosensory attenuation (Quattrocki and Friston, 2014), enhanced the strength of the RHI. Although the longevity of these effects is unclear (see Abdulkarim

et al., 2021, for evidence that they may last at least tens of seconds; cf. Heed et al., 2011; Kammers et al., 2009b for motor 'aftereffects' of the RHI), the overall conclusion of these behavioural studies is that the RHI is associated with, and can benefit from proprioceptive attenuation.

Unfortunately, only few brain imaging or electrophysiological studies have tested for deactivations by the RHI; i.e., for relatively attenuated brain activity during the illusion relative to its control conditions (Fig. 3C). Of those that did, however, each one has reported a negative relationship between the RHI and activity in the S1 contralateral to the targeted hand side: Tsakiris et al. (2007) reported decreased activity in the S1 specific to the RHI condition relative to a number of control conditions (interaction effect). Moreover, they found that the degree to which contralateral S1 and S2 activity was attenuated correlated with the amount of proprioceptive drift (a similar correlation was also observed in the hippocampus and cingulate cortex); i.e., a stronger attenuation of somatosensory activity was associated with a stronger bias in participant's judgments about the location of the hidden real hand towards the location of the visible rubber hand. As the proprioceptive drift is thought to indicate a recalibration of proprioception (see above), this result strongly suggests a link between proprioceptive attenuation and recalibration of the perceived hand position in the RHI.

Two studies (Limanowski and Blankenburg, 2016b; Zeller et al., 2015) have directly tested for lowered brain activity in the RHI compared with asynchronous stroking or incongruent real and rubber hand posture and compared with stroking of the real hand in full view. The idea behind this conjunction contrast was to identify brain areas that reduced their response specifically during *illusory* body ownership. Crucially, both evoked potentials (EEG, Zeller et al., 2015) and hemodynamic responses (fMRI, Limanowski and Blankenburg, 2016b) in the left S1 were suppressed when the right hand was subject to the RHI. In both studies, a similar pattern was observed in the right S1 when the left hand was used. Moreover, a follow-up network analysis using dynamic causal modelling showed that the reduced responses in the S1 were best explained in terms of a selective reduction of local neuronal gain, which in this type of network analysis is commonly interpreted in terms of reduced precision (Zeller et al., 2016). Together, these results clearly suggest that S1 activity is attenuated during the RHI, via attenuating precision. It should be noted that Gentile et al. (2013) found a (non-significant) increase in contralateral S2 activity during synchronous compared with asynchronous co-stimulation in a variation of the RHI paradigm. While this somewhat contradicts the idea of attenuation, it could be an effect of visuo-tactile stimulation rather than the RHI, since the S2 may be subject to cross-modal influences from the visual cortex. In sum, however, there is substantial evidence for an attenuation of activity in the contralateral somatosensory cortex during the RHI; and thus, for the idea of proprioceptive (precision) attenuation.

Following this idea, the S1 has been targeted by *brain stimulation studies*. Hornburger et al. (2019) found that, following a suppression of activity in the contralateral S1 via cathodal vs anodal transcranial direct current stimulation (tDCS), participant reported a stronger illusory self-attribution of the fake hand (but proprioceptive drift was not significantly affected). The authors concluded that disrupting somatosensory activity attenuated somatosensory precision, and thus helped to include the fake hand into the body representation. These results were nicely complemented by Frey et al. (2020), who found that increasing the excitability of the contralateral S1—corresponding to an increase in predicted precision—via iTBS *reduced* the reported strength of the RHI and the proprioceptive drift.

Similarly to the results of inhibiting the S1, Fossataro et al. (2018) found that interfering with contralateral M1 activity via repetitive transcranial magnetic stimulation (rTMS) increased illusion reports and proprioceptive drift. The M1 was also focussed by studies that investigated the excitability of the motor system during the RHI. Using TMS to the M1, della Gatta et al. (2016; cf. Miller and Farnè, 2016) found that the RHI was associated with a lower excitability of the M1, as measured by reduced amplitudes of motor-evoked potentials recorded from the

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Fig. 3. Visual vs proprioceptive cortical processing during the rubber hand illusion (RHI). **A:** In the RHI (schematic depiction following Botvinick, 2004), the participant sees a displaced fake hand being touched congruently with her real hand, which is hidden from view. In most participants, this has measurable consequences like a reported self-attribution of the fake hand, or a recalibration of the perceived real hand position towards the fake hand. **B:** Summary of recent meta-analyses of brain activity related to the experimental manipulation of 'body ownership' by variations of the RHI (statistical maps from Salvato et al., 2019 and Seghezzi et al., 2019, and peak activation overview from Grivaz et al., 2017, each reprinted with permission; white ellipses added). As shown, manipulations of body ownership have consistently been associated with increased activity in multisensory fronto-parietal areas (i.e., the premotor and posterior parietal cortex) and in the visual cortex (highlighted by white ellipses). These results suggest an enhanced visual information processing and multisensory integration during the RHI, which has been supported by connectivity analyses (Section 2.3.1). **C:** Studies that have tested for a potential *attenuation* of brain activity during the RHI suggest that the illusion may be associated with attenuated activity in the contralateral somatomotor cortex. This could imply that attenuating proprioceptive information fractificant effects on the strength of the RHI. Overall, these results support the proposed involvement of parietal and occipital regions in the RHI (cf. Section 2.3.1). Crucially, the results of studies targeting the contralateral somatomotor cortex clearly show that an inhibition of the S1/M1 enhances the RHI, whereas an excitation reduces it. The anatomical locations (MNI coordinates) of the respective significant peak effects of each study are indicated with coloured circles; dashed lines indicate peaks in the right hemisphere. CS = central sulcus, IPS = intraparieta

real hand subject to the illusion. In other words, the muscles of the hand were less readily activated during the RHI than during a control condition. Using a similar TMS paradigm in a non-RHI, visuo-proprioceptive conflict setting, Munoz-Rubke et al. (2017) also found M1 excitability to be inversely related to proprioceptive recalibration, but positively related to visual realignment. Interestingly, a study by Isayama et al. (2019), which also found altered M1 excitability during the RHI, suggested that this was likely the result of reduced gain of somatosensory afferents to the M1 from the S1 and the PPC. This interpretation is also supported by a paired pulse TMS study by (Karabanov et al., 2017), who found that, during a motor version of the RHI, connectivity from the anterior IPS to the M1 was inhibited (here, M1 excitability per se was unaffected, which might have been due to using a moving as opposed to static hand paradigm). Kanayama et al. (2017) found a positive correlation between the proprioceptive drift and the causal influence of the PPC on the contralateral S1 (using EEG), which could potentially fit the above interpretation; i.e., that the PPC might bias somatosensory processing in the S1.

2.3.3. Summary

In sum, the above brain imaging and electrophysiological results and the results of causal interventions via brain stimulation lend strong support to the idea that the RHI-the illusory incorporation of a seen, displaced fake hand into one's body representation-is associated with the attenuation of proprioceptive information from the real hand, and augmented visual information processing. In principle, the higher sensory precision of vision relative to proprioception (especially in a static setting where proprioception quickly degrades) could sufficiently explain the perceptual inference process leading to the RHI and its associated behavioural effects. The reviewed findings, however, suggest that this difference in intrinsic sensory precision may be further emphasized through top-down modulation (i.e., precision control). Thus, precision control, in particular the attenuation of proprioceptive information, can help to resolve visuo-proprioceptive conflicts under static sensory input. In the next section, we shall see that the same mechanism may help to recalibrate the body representation in order to adapt action planning to novel visuo-proprioceptive mappings.

2.4. Visuomotor adaptation

Visuomotor adaptation is another very popular experimental framework to investigate the flexibility of body representation. The principle of such experiments is to introduce a conflict between visual and proprioceptive body position information, by artificially displacing vision (which is, arguably, much easier than manipulating proprioception). For example, participants are exposed to reversed, rotated, or temporally delayed visual action feedback (Fig. 4A). Movements are typically measured via a computer mouse, joystick, or motion capture (e.g., data gloves); visual action feedback can be provided by a cursor or, in more ecologically valid scenarios, by videos or virtual reality models of a hand. To perform the (typically visuospatial) task under the introduced conflict, the participants have to learn a new mapping between executed movements and their visual consequences. Successful adaptation becomes evident through reduced movement error (i.e., participants get increasingly better at reaching the visual movement goal).

Visuomotor adaptation is a notably more complex scenario than the rubber hand illusion (Section 2.3). A key difference between the two paradigms is that visuomotor adaptation requires the integration of sensory feedback with motor commands for goal-directed action. However, for this to be efficient, sensory estimates from different available modalities must first be combined; which relies on the same mechanisms as discussed for the RHI (cf. Ghahramani et al., 1997). Correspondingly, similarly as the RHI, visuomotor adaptation is known to recalibrate the felt (i.e., proprioceptive) hand position towards the displaced visual cues (Harris, 1963; cf. Block and Bastian, 2011; Cressman and Henriques, 2009; Henriques and Cressman, 2012; Ostry and Gribble, 2016; Petitet et al., 2018; Rand and Heuer, 2019). This can, like the RHI, be described as the result of adjusting the visuo-proprioceptive body representation; i.e., in terms of a contextual (temporary) adjustment in visual vs proprioceptive information processing in the brain, potentially resulting from top-down precision control (Fig. 1).

As motor control requires adequately sensing one's body position,

applying the principle of proprioceptive attenuation here may seem even more paradoxical than in the case of the RHI. However, animal lesion studies and patient studies have revealed that proprioceptive deafferentation-the artificial removal or loss of proprioceptive sensation-does not necessarily preclude visuomotor adaptation. Although some deafferented patients were unable to adapt at all (Bard et al., 1995; Guedon et al., 1998), many studies have shown that, in visuomotor adaptation tasks, deafferented animals or participants performed comparably to healthy controls (Bernier et al., 2006; Ingram et al., 2000), or even outperformed them (Taub and Goldberg, 1974; Lajoie et al., 1992). There is tentative evidence for increased visual attention during early visuomotor adaptation, which decreases as performance improves (Reuter et al., 2015). This strategy may also be applied by deafferented patients, as they seem to be more strongly impaired by additional cognitive load (Ingram et al., 2000). Interestingly, degrading proprioception in healthy participants via wrist vibration, likewise, did not impair visuomotor adaptation (Pipereit et al., 2006). Based in parts on these observations, it has been speculated early on that removing or degrading proprioception may augment visuo-proprioceptive recalibration; by enabling a more efficient integration of new visual action feedback (Redding and Wallace, 1988; Harris, 1963; Kelso et al., 1975; Klein and Posner, 1974; Posner et al., 1978; Lebar et al., 2017; Liesner and Kunde, 2020; Tsay et al., 2021).

In the following section, I shall review recent evidence for this interpretation, focussing on brain imaging and stimulation studies that have investigated neuronal processes in the healthy brain during visuomotor adaptation. I shall particularly focus on the *early phase* of visuomotor conflict adaptation, where usually most of the behavioural adjustment is observed (e.g., Anguera et al., 2010; Harris, 1963; Inoue et al., 2000; Luauté et al., 2009; Yoon et al., 2014).

2.4.1. Cortical correlates

Several research groups have used brain imaging to localize activations associated with the early phase of visuomotor adaptation; using specific statistical contrasts, e.g., of brain activation during early relative to late periods of adaptation blocks, or linearly decreasing contrast weights throughout the blocks (Anguera et al., 2007, 2010; Graydon et al., 2005; Limanowski et al., 2017; Luauté et al., 2009; Seidler et al., 2006; Tzvi et al., 2020). These studies have consistently revealed an early activation of areas in the premotor, prefrontal, posterior parietal, and occipital cortex (Fig. 4B, cf. Table 1). Similar early fronto-parietal activity increases can be found in other studies, although these were not significant (or not tested for significance; Bédard and Sanes, 2014; Inoue et al., 2000). Interestingly, even over a week-long learning phase, adaptation performance during initial stages of learning was associated with significantly increased frontal and occipitotemporal activation in a PET measurement (Della-Maggiore and McIntosh, 2005). These are very similar to the regions activated by the RHI (Fig. 3B), although here the task seems to activate predominantly the dorsal visual stream--consistent with the idea that these areas are involved in the control of goal-directed reaching (Gallivan and Culham, 2015).

These results are complemented by *electrophysiological studies*. Perfetti et al. (2011) found increased gamma power over posterior parietal regions during the early phase of visumotor learning, interpreting it as the integration of new (visual) information for action planning. In a set of EEG studies on mirror tracing, Lebar et al. (2015, 2017) found enhanced visual evoked potentials (likely originating from the occipitotemporal visual cortex) and reduced oscillatory power in lower frequency ranges (8–12 Hz; i.e., 'alpha' and 15–25 Hz; i.e., 'beta') over posterior (visual) cortices during mirror-reversed vision. The authors interpreted these results as indicating a facilitated processing of visual inputs during visuo-proprioceptive incongruence. Very similarly, Reuter et al. (2015) found enhanced steady-state visual evoked potentials during visuomotor adaptation—notably, in particular during the early phase of learning (although this time-dependent effect was only observed for 60° but not 120° visual rotations). The authors likewise

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suggested that visual processing is facilitated during early adaptation; and specifically, that attentional mechanisms accomplish this.

It should be noted that most of the above brain areas typically show an overall activation increase during a visuomotor adaption block (Contreras-Vidal and Kerick, 2004; Grafton et al., 2008; Krakauer et al., 2004; Limanowski et al., 2017; Ogawa et al., 2006, 2007). However, the results discussed in this section suggest that they are activated particularly strongly during early learning.

2.4.2. Proprioceptive attenuation

Conversely, relatively few studies have investigated cortical activity decreases associated with visuomotor adaptation. Nevertheless, these studies paint a coherent picture. Brain imaging studies using PET have shown that activity in sensorimotor areas behaves inversely to what we have seen in the previous section; i.e., it is relatively lower during early stages of visuomotor adaptation, and increases throughout blocks: Inoue et al. (1997) showed that S1 activity was lower during early than during late visuomotor rotation adaptation (however, while the bilateral S1 was significantly activated during late adaptation vs a control reaching condition, only the right (ipsilateral) S1 showed a statistically significant difference between early and later periods of adaptation). Inoue et al. (2000) likewise reported lower activity during early relative to late visuomotor rotation adaptation in the contralateral supplementary motor area (SMA), and (although this difference was not statistically significant) in the contralateral S1. An analogous pattern of results was reported in the longitudinal (one week-long learning) study by Della--Maggiore and McIntosh (2005); i.e., adaptation performance was initially associated with increased activity in frontal and visual areas (see Section 2.4.1), but as learning progressed, it correlated increasingly with activity in sensorimotor areas (including the contralateral sensorimotor cortex and subcortical motor structures). In other words, the influence of sensorimotor information was, again, relatively attenuated in the early phase of adaptation.

Another approach was taken by Bernier et al. (2009), who measured somatosensory evoked potentials (SEPs) from the contralateral S1 during mirror tracing. During early visuomotor adaptation, the authors found a reduced amplitude of SEPs; which they interpreted as evidence for proprioceptive suppression, applied to allow novel visual information to be incorporated into the action plan. Corroborating the idea that such sensory 'gating' is particularly important during early learning, the attenuation of SEPs alleviated as performance increased over time. Notably, the authors did not find any modulation of peripheral and spinal evoked potentials, which further supports the idea that proprioceptive attenuation was happening directly within the S1.

Again, *electrophysiological results* corroborate the interpretation of the above results. In their EEG study with mirror tracing, Lebar et al. (2017) found a reduction of oscillatory power in higher frequency ranges (50–80 Hz; i.e., 'gamma' and 15–25 Hz; i.e., 'beta') over sensorimotor areas (in addition to the simultaneously observing reduced lower-frequency oscillatory power over visual areas, see Section 2.4.1). In line with accounts that associate high oscillatory frequencies with bottom up sensory processing, and low frequencies with top-down modulations (Bastos et al., 2015; Fries, 2001; Wang, 2010), the authors interpreted this diametrical change as increased visual gain and reduced integration of somatosensory inputs. These results, and their interpretation, are very much in line with the findings discussed in Section 2.2, i.e., that visual vs proprioceptive sensory gain can be diametrically changed depending on the currently active 'attentional set' (Limanowski et al., 2020; Limanowski and Friston, 2020a).

Finally, further evidence for the idea that proprioceptive attenuation benefits learning comes from differences in the after-effects of visuomotor adaptation (i.e., action biases that persist after returning to 'normal' vision). Goldenkoff et al. (2021) showed that participants exposed to reversed visual feedback during an adaptation and transfer task exhibited attenuated SEPs following training. This result complements the classical findings of Taub and Goldberg (1974), who showed



Fig. 4. Visual vs proprioceptive cortical processing during visuomotor adaptation. **A:** Exposure to novel visuomotor mappings is typically realized by artificially displacing vision; i.e., introducing a conflict between executed, felt movements (proprioception) and seen movements (vision). This can be done by rotating or mirroring visual action feedback, or by introducing temporal delays to it (in the example shown here, visual feedback is rotated by 45°). Adaptation to the novel visuomotor mapping means learning to adjust movements to complete the desired action (pointing to the target), which itself requires adequately integrating multisensory action feedback into the body representation. **B:** Summary of cortical activity increases during early phases of visuomotor adaptation (where most of the adjustment typically takes place, see main text). The peaks roughly accumulate in the prefrontal and premotor cortex, the posterior parietal cortex (PPC) along the intraparietal sulcus (IPS), and in the visual cortex (LOC = lateral occipitotemporal cortex; CS = central sulcus). These results suggest an early prioritized processing of visual action feedback for integration with internal models for action control. **C:** Studies that have tested for activity decreases during visuomotor adaptation tasks suggest that a temporary attenuation of activity in the somatomotor cortex may facilitate adaptation. **D:** Artificially inhibiting activity in the S1 via brain stimulation has correspondingly been linked to enhanced adaptation. The anatomical locations (MNI coordinates) of the respective significant peak effects of each study are indicated with coloured circles; dashed lines indicate peaks in the right hemisphere. See Table 1 for details.

that prism aftereffects were substantially larger for deafferented than for healthy monkeys; as noted before, the authors interpreted this as evidence for the idea that removing proprioception augments visuo-proprioceptive recalibration.

Another route to investigating the effects of proprioceptive attenuation on visuomotor adaptation was taken in *brain stimulation studies*. Balslev (2004) applied rTMS to the putative S1 (contralateral to the used hand) in order to inhibit somatosensory (i.e., proprioceptive) information processing. They showed that this reduced proprioceptive acuity (as measured with a position matching task), but at the same time significantly *improved* mirror-view tracing (i.e., visuomotor adaptation) during early learning trials. Yoon et al. (2014) likewise showed that rTMS inhibition of the contralateral S1 improved visuomotor adaptation; specifically, that it increased the shift of proprioception towards vision (although this effect was only significant under terminal, not under continuous visual feedback).

2.4.3. Summary

Overall, the above brain imaging, electrophysiological, and brain stimulation results point to augmented visual processing and attenuated proprioceptive processing during visuomotor adaptation, in particular during its early phase; as evident from the clear localisation of significant effects to brain areas processing visual vs proprioceptive body information. These results support the idea that a temporary proprioceptive (precision) attenuation may augment visuomotor adaptation. Thus, we can conclude that precision control may not only keep the body representation intact during static visuo-proprioceptive conflicts, but that it also helps to learn how to act under such conflicts.

3. Conclusion and outlook

The aim of this review was to evaluate the idea that precision control allows the flexible adaptation of the brain's visuo-proprioceptive body representation; specifically, through the selective attenuation of the precision assigned to proprioceptive information. In Section 2.2, we have seen that the cortical processing of visual vs proprioceptive body position information can, in principle, be altered top-down by cognitive factors such as attentional 'sets'. This supported the assumption that sensory information flow used to construct the own body representation can be gated based on top-down modulation. Building up on this, Sections 2.3 and 2.4 have reviewed empirical research on visual vs proprioceptive processing in static (rubber hand illusion) and dynamic (visuomotor adaptation) settings. Overall, the reviewed literature showed that mismatching visual body position information can be more easily incorporated into the brain's body representation if proprioception is attenuated. The effects of attenuating proprioception were clearly localised to the primary somatomotor cortices contralateral to the used hand side. As we have seen in Section 2.4, proprioceptive attenuation (and visual enhancement) may be particularly relevant during the early phase of such adaptation; which tentatively supports the idea that, once adaptation has been achieved, top-down modulation (i.e., precision control) may be relieved again (cf. Fig. 1D).

In sum, the reviewed findings fit well into the predictive coding framework, which postulates a close link between attention, precision, and neuronal gain (Box 1). With the top-down control over precision as formulated by predictive coding, we have a plausible candidate mechanism that could reveal more about how the brain accomplishes flexibility in the body representation. The search for mechanisms is essential, because computational accounts of how body models are learned and updated are still in their infancy. While precision control is certainly not the sole mechanism of flexible body representation, the reviewed literature underlines its potential to resolve bodily uncertainty, especially under intersensory conflict or in novel multisensory environments. In other words, by augmenting or attenuating sensory (bodily) precision depending on e.g. the current context or goals, people can exert a certain degree of control over how strongly different kinds of sensory information update their body model.

The idea of precision control as a mechanism for flexible body representation opens up a number of interesting questions and research directions. For instance, bodily uncertainty in the face of visuoproprioceptive conflicts could, in principle, also be reduced by attenuating *visual* precision. That visual bodily input can be contextualised has been shown by psychophysics and brain imaging studies, in which visual action feedback was attenuated during active vs passive movements (Vasser et al., 2019; Limanowski, Sarasso et al., 2018). Work on audiovisual integration has shown that increased sensory precision may enhance the sensitivity to the spatial disparity of the individual cues and, thus, potentially narrow the limits of their integration (Rohe and Noppeney, 2015a,b). In line with this idea, Chancel et al. (2021) have recently found that the addition of visual noise enhanced the RHI in a VR

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setting. This could suggest that lowering visual precision, despite decreasing the relative dominance of vision over proprioception, might increase the probability of inferring a common cause, thus facilitating visuo-proprioceptive integration. While Chancel et al. experimentally introduced sensory noise (i.e., changing precision 'bottom-up'), it would be interesting to see if similar effects on causal inference can be achieved through top-down attenuation of visual precision (i.e., precision control); for instance, resulting from attentional manipulations.

Future work should also investigate precision control and sensory attenuation during bodily conflicts across other sensory domains. For instance, during visuo-vestibular conflicts in heading perception tasks, one can observe a similar recalibration of the vestibular sense towards displaced vision, which likewise seems to depend on differences in sensory precision (Acerbi et al., 2018; de Winkel et al., 2017). Therefore, it would be interesting to examine if top-down precision control may also augment this process.

Another open question relates to the finding that in some audiovisual (Talsma et al., 2007; Mozolic et al., 2008) and visuo-tactile (Badde et al., 2020) experiments, attending to only a single modality may inhibit or delay multisensory integration in certain settings. The seeming contrast with the reviewed evidence for enhanced visuo-proprioceptive conflict resolution under proprioceptive attenuation can be explained in two ways. Firstly, Badde et al. (2020) suggested that their results might be explained by a relatively weak, flexible prior about visuo-tactile unity; as a consequence, attention to both modalities was needed "to evaluate whether signals that are not currently relevant originate from the same source" (p. 11). In contrast, people may have a tendency to integrate visual and proprioceptive bodily cues (within certain limits) due to a strong natural prior about bodily unity, as postulated by recent work on body representation (see Introduction). In fact, the strength of this prior may be a reason for why proprioceptive attenuation is applied at all; i.e., because otherwise the conflicting proprioceptive body information would be too difficult to ignore. Secondly, given the crucial importance of proprioception for body perception and action (cf. Introduction), it is unlikely that proprioceptive information can be completely ignored; especially when movement is required (Section 2.4). In this light, precision control (attention or attenuation) should be seen as balancing the relative situational influence of proprioception vs vision on the body model, rather than implying a complete ignorance of either modality (which may be the case in other, non-bodily scenarios). This would also fit with the result of Badde et al. (2020); i.e., that the recalibration of perceived tactile towards displaced visual stimuli increased when tactile precision was somewhat reduced, whereas strongly attenuated tactile precision abolished this effect. The key question for future work is to determine how strongly and how persistently proprioception can be attenuated, e.g., in the RHI or in visuomotor adaptation.

On a neuroanatomical level, subscribing to the assumption that precision control is implemented through the top-down modulation of neuronal gain in sensory brain regions, future work should aim to identify the 'higher-level' sources of these modulatory effects (i.e., brain areas issuing the corresponding predictions of precision). This would be an important step in mapping the mechanistic (computational) architecture of body models to known neuroanatomy. For instance, some evidence suggests that the PPC might bias somatosensory processing in the S1 (Section 2.3.2), but there are many possible cortical and subcortical candidates.

Together, answering the above questions could contribute to a new mechanistic understanding of body representation and its alterations or disorders. For instance, it may explain the potential "disembodiment" of the own limb during the RHI (for discussions, see della Gatta et al., 2016; Longo et al., 2008; Miller and Farnè, 2016) as resulting from particularly strongly attenuated proprioceptive precision. Task settings involving visuo-proprioceptive conflict resolution may also offer ways to treat bodily disorders. For instance, in patients with hemispatial neglect, prism adaptation may lead to an improvement in visual and cognitive

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symptoms and, interestingly, also in improved contralesional somatosensory perception (Maravita et al., 2003; Dijkerman et al., 2004). This has been interpreted in terms of an activation of multisensory spatial-attentional mechanisms, which are otherwise impaired in hemineglect, through the visuomotor task (Maravita et al., 2003). Thus, rather than contradicting the idea of augmenting adaptation through proprioceptive attenuation, these findings may indicate that flexible precision control can be re-learned in appropriate task designs.

Understanding precision control and sensory attenuation in the body representation may also help to tackle the challenges that are arising with the increasing amount of new forms of action and interaction through surrogate (e.g., virtual or robotic) bodies. This is a case in which we can find intersensory bodily conflicts outside of the artificial settings used in the reviewed experiments: Due to current technological limitations of virtual (or augmented) reality, the user often finds she has to ignore sensations that 'remind' her of the physical reality (such as the weight of a VR-headset, or slight lags in the movements of an avatar) to convincingly immerse into the 'competing' virtual reality (Slater et al., 2020; Vasser and Aru, 2020). Perhaps this can also be described in terms of precision control; i.e., as a selective attenuation of the precision assigned to certain (bodily) sensory information to adopt an alternative bodily 'reality'. Such an understanding would greatly help assess the benefits and potential dangers of modern cyber-physical interactions.

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