

Cortical candidates for self-other distinction based on visual and action cues: Where do we stand?

Jakub Limanowski

Institut für Psychologie, Universität Greifswald, Greifswald, Germany

Correspondence: Jakub Limanowski, Universität Greifswald, Institut für Psychologie, Franz-Mehring-Straße 47, 17489, Greifswald, Germany, Phone: +49 (0)3834 420 3725, Email: jakub.limanowski@uni-greifswald.de

Abstract: Distinguishing sensations that were generated by one's own actions from those that were not may be grounded in the evaluation of sensory (re)afference against motor predictions by “comparator” modules in the brain. Brain imaging studies have converged on three candidate brain regions for self-other distinction based on such a comparison of visual and action cues: the EBA, the STS, and the AG. Yet, the question whether the “action cues” received by those regions are motor or non-motor cannot conclusively be answered due to the heterogeneity of the imaging results and differences in experimental methodology. Thus, there is an ongoing debate which of these regions implement visuomotor comparisons, or merely intersensory (visuoproprioceptive) comparisons blind to the cause of movement. In this mini review, I revisit the assumptions of classical visuomotor comparator models; discuss potential experimental biases resulting from non-motoric cues; highlight how differences in kinematic predictability result from different kinds of visual distortion—and how this could be capitalized on; and discuss the potential promises and pitfalls of recent experimental approaches using factorial visuomotor conflict designs with additional control over the locus of movement generation.

Key words: Action; comparator model; motor control; self-other distinction; vision

Introduction

Perceiving myself as distinct from others fundamentally relies on distinguishing sensations that were generated by “me” (i.e., the sensory consequences of my actions) from those that were generated by external causes (e.g., other agents). This allows for the construction of adaptive models in the brain that distinguish self-generated from externally generated sensations to more efficiently guide and correct the organism’s action in a changing environment (Graziano & Botvinick, 1999; Wolpert & Flanagan, 2001; Jeannerod, 2003; de Vignemont & Fournieret, 2004; Gallese & Sinigaglia, 2010; Limanowski & Blankenburg, 2013; Apps & Tsakiris, 2014). 5-month-old infants can already discriminate between self-produced visual body movements and those produced by other infants (Bahrick & Watson, 1985). A differential processing of matching vs mismatching visual kinematics has been well documented in adults as well (e.g., Tsakiris et al., 2005; Brass et al., 2009; Salomon et al., 2013; Yon et al., 2018). Conversely, pathologies like in some forms of schizophrenia hint at the profoundly negative consequences that a failure to distinguish between self- and other-generated sensations may have for embodied selfhood (Frith et al., 2000; Synofzik et al., 2010; Brown et al., 2013; Schmitter et al., 2025).

Computational architectures known as “comparator models” (see Section “Neurocomputational architectures for self-other distinction based on visual and action cues”) formulate how the comparison of sensory movement consequences with motor predictions in the brain underlies conscious self-other distinction and agency attribution (Blakemore et al., 1998; Gallagher, 2000; Frith et al., 2000; Synofzik et al., 2008a; Haggard, 2017). Of course, depending on its definition, the construction of a conscious “sense of agency” likely involves many more processes than sensorimotor comparisons, with different neuronal implementations (de Vignemont & Fournieret, 2004; Synofzik et al., 2008a; Grünbaum & Christensen, 2017; Wen, 2019; Moore & Fletcher, 2012). For instance, self-other distinction can also be attempted based on sensory data alone (i.e., inference about passive “body ownership” (Paillard, 1999; Jeannerod, 2003; Tsakiris, 2010; Tsakiris et al., 2010). However,

this inference is blind to the *cause* of the sensory data: Seeing a body movement does not per se tell me whether it is a consequence of *my* action I am seeing or of someone else's. This kind of self-other distinction can only be achieved by comparing “visual and action cues” (Jeannerod, 2004). Thus, most of the above accounts agree on that the comparison of predicted and actual movement feedback (reafference) by comparators in the brain is one of the first and most important steps in establishing conscious self-other distinction. It is these comparisons—specifically, visuomotor comparisons—and their neurofunctional basis that are the focus of the present review.

Manipulations of visual movement feedback (i.e., its congruence with motor signals) belong to the most popular approaches to studying sensorimotor self-other distinction (Jeannerod, 2003; Grünbaum & Christensen, 2017; Wen, 2019). Neuroimaging approaches to visuomotor self-other distinction have used various experimental manipulations of visual movement feedback, and the resulting brain activity increases have been interpreted in line with the comparator model; i.e., as indicating mismatch (error) processing as a potential first step in self-other distinction.

However, due to methodological differences and difficulties (see below), many key questions about visually based self-other distinction remain open, including where the “comparator module” is located in the brain and what kind of signals the visual input is compared against. Here, after a brief primer on the classical “comparator” models underlying sensorimotor self-other distinction in the brain, I shall revisit proposals converging on three key candidate areas for visuomotor comparisons in the brain, and briefly summarize the relevant key empirical findings. Then I shall review the most popular manipulations of visual movement feedback, focusing on their differences regarding the predictability of visual kinematics from motor signals and what this implies for the experimental isolation of visuomotor comparisons from non-motoric cues. Finally, I review human brain imaging studies that have combined manipulations of visual movement feedback with adaptation designs, and with manipulations of the locus of movement generation (internal vs external), and discuss what these approaches mean for

isolating tentative visuomotor comparators. I shall end with a summary of the key open questions, alongside some suggestions as to how to proceed.

Neurocomputational architectures for self-other distinction based on visual and action cues

Computational approaches to self-other distinction and its neurobiological implementation have largely been inspired by models from the motor control literature commonly referred to as “comparator models” (Blakemore et al., 1998; Gallagher, 2000; Frith et al., 2000; Synofzik et al., 2008a). In short, these models rest upon the idea of that, upon movement execution, the motor system sends a copy of the motor commands (Sperry 1950; von Holst & Mittelstaedt 1950; cf. Weiskrantz et al., 1971) to an internal “forward” model, which uses it to generate a prediction of the sensory consequences resulting from the execution of the intended (body) movement (Wolpert & Miall, 1996; Desmurget & Grafton, 2000; see Fig. 1A). These forward predictions can be used for state estimation and error correction instead of the actual sensory feedback, which reaches the brain only after substantial delays (Miall & Jackson, 2006; Leib et al., 2024). This is a great benefit for sensory-guided action control (i.e., feedback control), because the correction of actions can now be based on anticipated sensory errors rather than having to wait for the actual sensory reafference.

Moreover, these predictions can be used to distinguish predicted reafference (i.e., the sensations generated by action) from unpredicted sensations (Wolpert & Flanagan 2001). Thus, a “comparator module” evaluates the actual, incoming sensory reafference against the (delayed) forward prediction issued by the motor system’s forward model (Fig. 1A). If this comparison results in a mismatch (prediction error), it means that the sensory feedback was unpredicted by one’s motor system and, therefore, likely not self-generated (Gallagher, 2000; Frith et al., 2000; Jeannerod, 2003; Synofzik et al., 2008a; Haggard, 2017; Grünbaum & Christensen, 2017). The predicted reafference can be processed differently than unpredicted (exafferent) signals, which is important for contextually flexible motor control (see below).

97 The neurophysiological basis of motor/visuomotor control has been covered by several
 98 excellent reviews (e.g., Shadmehr et al., 2010; Wolpert & Miall, 1996; Scott, 2012; Adams et
 99 al., 2013; Archambault et al., 2015). While any single brain region could play a role in more
 100 than one kind of computation, there are several fitting candidates implementing specific
 101 computations based on their connectivity and known activity: The generation of motor plans
 102 and commands or predictions are likely implemented by premotor and primary motor areas,
 103 while forward models and state estimators may be implemented by the cerebellum and the
 104 posterior parietal cortex (Blakemore & Sirigu, 2003; cf. Tzvi et al., 2022; Quirmbach &
 105 Limanowski, 2024; Kilteni & Ehrsson, 2024). These are likely supplemented by structures
 106 evaluating costs and rewards in, e.g., the basal ganglia (Scott, 2012).

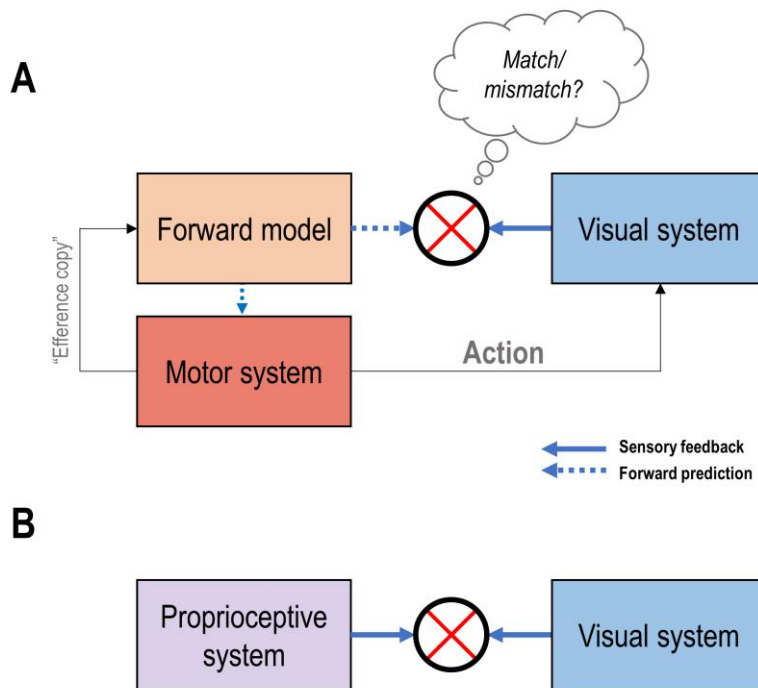


Figure 1. A: Simplified depiction of the “comparator model”. In parallel to generating action and the ensuing sensory (in this case, visual) movement feedback, the motor commands are fed as a copy to a “forward model” that uses them to predict the expected sensory (e.g., visual) movement consequences. These forward predictions can be used by the motor system for state estimation and “on-line” control instead of the actual sensory feedback, thus overcoming the problem of intrinsic conduction delays. Importantly, the sensory forward predictions can also be evaluated against the actual visual movement feedback (“reafference”) by a “comparator” module (crossed circle). Matches indicate correct predictions and, thus, likely signal self-generated movement consequences, which can be attenuated or “filtered

out”. In contrast, mismatches mean that the observed movement was at least partly unpredicted, and therefore, likely generated externally (e.g., by someone else). This comparison fundamentally depends on the comparison of motor signals for action with sensory reafference. **B:** Another way to evaluate whether observed movements are of one’s own body. The seen limb position can be compared with its position conveyed by proprioceptors in the muscles and tendons (provided the appropriate transformations e.g. between the different coordinate systems used by vision and proprioception). Despite not receiving any motor signals, the detection of visuo-proprioceptive mismatches may also signal that the observed movement likely does not “belong” to one’s body, and can thus, in principle, also contribute to visually based self-other distinction of movement.

Most frameworks or hypotheses of self-other distinction assign “comparator” modules in the sense of Fig. 1A to the cerebral cortex. Thereby, a cortical visuomotor comparator should meet three criteria: Firstly, it should process visual movement feedback; i.e., it should receive afferents from earlier (primary or thalamic) visual areas and show activation by observation of visual body movements. Secondly, it should receive forward predictions of visual movement feedback (see above) from the motor system; e.g., from the cerebellum, the PPC, or other (pre)motor cortices. Thirdly, the candidate brain area should respond differently to visual movement feedback that matches the forward predictions vs to feedback that violates them.

Commonly, it is assumed that comparator modules in the sense of Fig. 1A signal mismatches (see above, e.g., Gallagher, 2000; Frith et al., 2000; Haggard, 2017). I.e., the prediction errors resulting from mismatching (i.e., unpredicted) sensory movement feedback are thought to be reflected by increased activity, e.g., increased hemodynamic responses in the comparator (e.g., Blakemore et al., 1998; Leube et al., 2003). This relates to the idea that self-generated sensory movement feedback is attenuated (e.g., Brown et al., 2013; Palmer et al., 2016; Kilteni & Ehrsson, 2004). It should be noted, however, that self-generated (e.g., visual) feedback can also be augmented depending on task or control demands, which suggests more flexible, contextual gain control in the sensorimotor system (Scott et al., 2015; Azim & Seki, 2019; Limanowski, 2022). A possible reconciliation is offered by “sharpening” accounts suggesting increased neuronal activity, but only in a small proportion of neurons tuned to the self-

generated sensory data (Yon et al., 2018; Reznik & Mukamel, 2019). This could imply sequential, contextually weighted processing of expected and unexpected sensory information for optimal learning (Press et al., 2020). In this review, I follow the classical assumption that comparators can be identified through their increased responses to unpredicted sensations, although this assumption may need to be revisited in light of the above (Box 1). Other, complementary or subsequent processes such as the conscious self-attribution of action outcomes (“agency”) may be implemented by entirely different brain regions, such as the insula (Seghezzi et al., 2019; Sperdutti et al., 2019; cf. Haggard, 2017).

There is another key constraint on identifying visuomotor comparators, because, as noted, another kind of comparison of visual movement signals may also contribute to self-other distinction independently of motor signals and ensuing forward predictions: The seen limb position can be compared with its position conveyed by proprioceptors in the muscles and tendons—provided the nervous system has calculated the appropriate transformations between the different coordinate systems used by vision and proprioception (Fig. 1B, Weiskrantz et al., 1971; Makin et al., 2008; Tsakiris, 2010; van Kemenade et al., 2019). In the simplest case, this means a momentary comparison of static visual and proprioceptive ‘snapshots’ of limb position, perhaps also informed by postural priors such as e.g. the “body schema” (specifying possible bodily states given the current configuration, Head & Holmes, 1991; Paillard, 1999; Bermúdez, 2001; Synofzik et al., 2008b). Monkey neurophysiology and human imaging studies have identified neural correlates of such static visuo-proprioceptive comparisons in the PPC, the premotor cortex, the EBA, and the cerebellum (Graziano & Botvinick, 1999; cf. Ehrsson et al., 2004; Limanowski & Blankenburg, 2016; Zimmermann et al., 2016). The detection of mismatches between predicted and sensed visual vs proprioceptive limb posture may be a “non-motoric bodily cue” for self-other distinction, signaling that the observed movement likely does not “belong” to one’s body (Villa et al., 2022; cf. Bermúdez, 2001; Jeannerod, 2004). Crucially, however, this process is blind to the source of one’s body movements; and, as such, cannot identify whether an seen movement was self-*caused* or not (see above).

Naturally, sensory based and sensorimotor comparisons are tightly linked in determining body ownership and agency in most scenarios. A key challenge for imaging studies trying to locate ‘true’ visuomotor comparisons in the brain—according to the three criteria above—is to control for the neuronal correlates of such “non-motoric”, intersensory comparisons. Several studies have attempted to do this, identifying brain regions possibly implementing comparators in the sense of Fig. 1A.

Possible loci of visuomotor comparisons in the brain

Visuomotor comparisons can, in principle, be calculated in all regions receiving visual and motor signals—but a few particularly fitting candidate regions have been identified. One of the first neurocognitive models for self-other distinction based on visual and action cues was proposed by Jeannerod (2004): In this model, the “extrastriate body area” (EBA, Downing et al., 2001) can distinguish self-produced body movements from those of others, whereby this information may then be used by the angular gyrus (AG) in the inferior posterior parietal cortex (PPC) for the self- or other-attribution of action. Based on the signals from the EBA, the STS and premotor cortex could evaluate the social significance and intentions underlying the observed actions.

Jeannerod’s proposal drew upon the already well established role of the AG—more broadly, the inferior parietal lobule (IPL)—in the self- or other-attribution of action consequences (e.g., Sirigu et al., 1999; Farrer & Frith 2002; Farrer et al. 2003). The AG, among other regions, has been associated with self-other distinction the wider concept of the “sense of agency” by many studies (see the excellent reviews by Decety & Lamm, 2007; David et al., 2008; Sperduti et al., 2011; Zito et al., 2020; Seghezzi et al., 2021). Van Kemenade et al. (2017) have proposed a “supramodal” (domain general) comparator in the AG, which is supported by other recent findings of it showing multimodal action-outcome mismatch responses (Balslev et al., 2006; Ogawa et al., 2007; Krugwasser et al. 2019). This notion also aligns with the classification of the AG as a higher-level, multi-modal association cortex based on its extensive connectivity profile (cf. Passingham et al., 2002): AG connections include inputs from striatal, thalamic, and

brainstem systems; short-range connections to parietal, occipital, and temporal lobes; and long-range connections to frontal association cortices (Petit et al., 2023; Yakar et al., 2023; Rockland, 2023; Humphreys & Tibon, 2022). Furthermore, AG activity covaries with premotor, parietal, and cerebellar activity, which could suggest functional connectivity with key sensorimotor control regions (Uddin et al., 2010; Mars et al., 2011).

Alternatively, visuomotor comparisons could be implemented in specialized brain areas. Thus, a prominent hypothesis is that visuomotor comparisons should be implemented by brain areas processing visual motion—specifically *visual biological motion*; i.e., that of living bodies (Jeannerod, 2003, 2006; Kilner et al., 2007; Peelen & Downing, 2007; Friston et al., 2011). Models of biological motion have classically focused onto higher-order visual areas in the ventral stream; specifically areas in the lateral occipitotemporal cortex (LOTC) including the EBA and hMT+, and inferior temporal regions in the STS (Perrett et al., 1985; Grossmann et al., 2000; Puce & Perrett, 2003; Giese & Poggio, 2003; Lange & Lappe, 2006; Blake & Shiffrar, 2007).

Thus, a prominent model (Giese & Poggio, 2003) proposed two parallel processing streams, for form (processing sequences of visual “snapshots”, linked to ventral areas) and motion (processing optical flow, linked to dorsal areas), which converge on neurons in the STS. In this model, the EBA has been initially classified as part of inferotemporal areas in the “form” pathway; i.e., processing visual “snapshots”. This resonates with another model by Lange and Lappe (2006), which proposed serial processing of form in the EBA and, subsequently, of global motion in the STS. The EBA is hence seen as an important part of the biological motion perception network, but associated primarily with the static analysis (of body posture) in sequential frames. Similarly, based on systematic comparisons of motion processing in the EBA vs the STS it has been argued that the EBA analyzes visual information of body posture in static snapshots (Vangeneugden et al., 2014; cf. Kontaris et al., 2009). This would render it an unlikely visuomotor comparator. However, developments of the Giese & Poggio model have proposed interactions between both streams prior to STS (Peuskens et al., 2005); and have

aligned the EBA's role more with that of the STS – locating it in the “motion” rather than the “form” pathway, with input from MT and other motion sensitive visual regions (Giese, 2015). This aligns with findings suggesting that configurational and kinematic visual body motion information are integrated in the EBA (Jastorff & Orban, 2009). In sum, while biological motion perception involves many more areas including motion sensitive areas hMT+ and the kinetic occipital area (Grossmann et al., 2000; Vaina et al., 2001), the STS and EBA are good candidates for processing visual biological motion in a way a potential “comparator” would need to.

However, the EBA and STS could also simply respond to visuo-proprioceptive mismatches (Fig. 1B); i.e., without evaluation against motor signals. Indeed, it is well documented that the EBA is sensitive to visuo-proprioceptive congruence even in the absence of movement; e.g., as demonstrated by studies on visuo-proprioceptive arm position integration (Ehrsson et al., 2004; Makin et al., 2008; Tsakiris, 2010; Limanowski & Blankenburg, 2014, 2016; Zimmermann et al., 2016). In contrast, the STS does not seem to respond to visuo-proprioceptive incongruence in the absence of movement (i.e., in static comparisons). This suggests any ‘mismatch’ response in the STS during mismatching visual movement feedback is likely unrelated to visuo-proprioceptive conflicts per se, and would be a strong argument for visuomotor (biological motion) comparisons in the sense of Fig. 1A.

A potential motor role of the EBA has been suggested by the seminal findings of Astafiev and colleagues (2004), who demonstrated that the EBA was activated by unseen own body movements (see Limanowski & Blankenburg, 2016, for a similar result). This was interpreted as potentially indicating the reception of motor signals such as an efference copy (e.g., Jeannerod, 2004). The proposal of visuomotor self-other distinction in the EBA¹ has since received quite some support—most notably, from studies associating EBA responses with the

¹ In this review, I stick with the label “EBA”, “AG”, and “STS” for consistency with these previous proposals (Jeannerod, 2004; David et al., 2007). It should be mentioned that not all of the reviewed studies functionally localized the EBA; hence a broader label would be “lateral occipitotemporal cortex” (Lingnau & Downing, 2016). Similarly, I consider reported hemodynamic activations with peaks in or around the AG or STS; i.e., also discussing those in the respectively neighboring SMG or superior temporal gyrus.

processing of mismatching visual movement feedback (e.g., David et al., 2007, 2009, Yomogida et al., 2010; Limanowski et al., 2017; see David et al., 2008, Zito et al., 2020, for reviews). But it has also been challenged on many accounts (see e.g. the reviews by Peelen & Downing, 2007; Lingnau & Downing, 2015), partly drawing on the functional definition of the EBA as a classical category-specific ventral stream region based on its significant preference for visual stimuli that depict human body parts (Downing et al., 2001). Thus, there is an ongoing debate about whether the EBA processes dynamic or static movement signals (see above); and whether the information it possibly receives about own body movement beyond vision is of motor (i.e., corollary discharge) or sensory (i.e., proprioceptive) nature. As the EBA is a functionally, not cytoarchitecturally defined region (Lingnau & Downing, 2015), the main insights about its connectivity stem from functional or effective connectivity studies. These studies have shown correlated activity of the EBA and the PPC (Limanowski & Blankenburg, 2014, 2017; Zimmermann et al., 2018; Moayed et al., 2021). Zimmermann et al. (2018) found that, functionally and structurally, the EBA was more strongly connected to dorsal stream regions than other category-selective ventral stream regions. These results align with a potential motor role of the EBA (see above and Zimmermann et al., 2016).

The STS is the most consistently emphasized region in models of biological motion perception (see above). This region shows strong responses during action observation, and has been associated with social perception from visual cues, including imitation from observation (Allison et al., 2000; Iacoboni et al., 2001, 2005). Recent models even suggest it as a core node in a possible third visual stream, in between the classical ventral and dorsal ones, which underlies the unique social abilities of humans (Pitcher & Ungerleider, 2021; Patel et al., 2019). Notably, the STS's strong responses during passive action observation can also be interpreted as indicating self-other distinction based on the comparison of one's (absent or contrary) motor signals with the seen action (Leube et al., 2003; Kilner et al., 2007; cf. Frith & Frith, 1999; Miall, 2003). In line with this idea, several human brain imaging studies have found increased responses in the STS, not in the EBA (or AG), to mismatching visual movement feedback (Leube et al., 2003; Iacoboni et al., 2005; Kontaris et al., 2009; Limanowski, Sarasso et al.,

2018). As in case of the EBA (see above), a common interpretation of the STS is as a non-
 motor region; i.e., as lacking motor properties, in contrast to other, parieto-frontal regions
 (Rizzolatti & Sinigaglia, 2010). The STS may receive afferents from the ventral stream areas
 (i.e., from the EBA/hMT+ and other temporal regions; cf. Giese & Poggio, 2003; Dasgupta et
 al., 2017; Patel et al., 2019), but also from the PPC (Yeterian et al., 1991; Seltzer et al., 1994,
 but note that these results were obtained in monkeys); while it projects frontal (premotor) areas
 (e.g., Luppino et al., 2001). As shown for the EBA (Zimmermann et al., 2018, see above), a
 meta-analysis showed that the posterior STS coactivated more strongly with dorsal stream
 regions; i.e., the PPC and pre- and supplementary motor areas (Erickson et al., 2017).
 Likewise, some studies reported STS activation by movements without vision (Molenberghs et
 al., 2010; Limanowski, Sarasso et al., 2018).

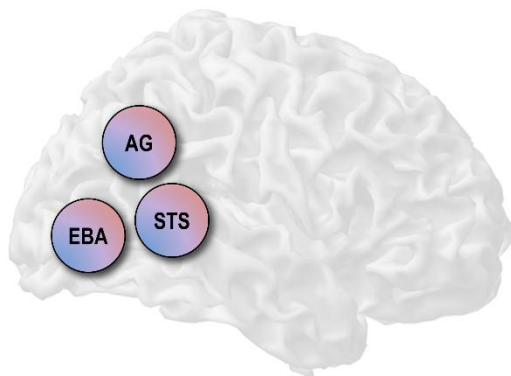


Figure 2: Three candidate regions for the implementation of self-other distinction of body movements based on visual and action cues. All three regions are activated by action observation, show elevated responses to distorted visual movement feedback, and potentially receive motor signals. EBA = extrastriate body area; STS = superior temporal sulcus; AG = angular gyrus.

In sum, of the regions proposed in Jeannerod's model, the AG, the EBA, but also the STS are
 promising potential candidates for visually based self-other distinction of action (Fig. 2). Firstly,
 all three regions are activated by action observation (see Caspers et al., 2010, for a meta-
 analysis); i.e., they process visual body movements. Secondly, a recent meta-analysis of
 human fMRI studies (Zito et al., 2020; cf. also Sperdutti et al., 2011) identified hemodynamic
 correlates of "negative agency" in visuomotor tasks confined to essentially only these three
 brain areas (AG/inferior PPC, STS, and occipitotemporal clusters potentially encompassing
 the EBA). This aligns with the assumed sensitivity of these regions to visuomotor mismatches.

However, only few published imaging studies used designs suited to isolate visuomotor from visuo-proprioceptive comparisons (see below). Thus, the key question remains: Which of these brain areas, if any, uses motor afferents to ascribe visual movement feedback to oneself or others.

Importantly, all three candidate areas could, potentially, receive motor signals based on their known functional and structural connectivity: The motor role of the PPC is undisputed (Wolpert et al., 1998; Andersen & Buneo, 2002), and the anatomical and functional connectivity of the AG suggests several possibilities of receiving motor signals from e.g. parietal, premotor, or potentially even cerebellar areas (Mars et al., 2011; Uddin et al., 2010; see above). However, although there is some evidence for at least functional coupling between the EBA/STS and motor regions like the premotor or parietal cortex (e.g., Patel et al., 2019; see above), it is still an open question whether the EBA and the STS receive motor signals e.g. from regions implementing forward models (Box 1).

In sum, the exact function of the AG, EBA, and STS in visuomotor self-other distinction is still not fully clear. Besides open questions about network activity/connectivity, this is predominantly due to the heterogeneity of the published functional results (see van Kemenade et al., 2019, for a discussion). This heterogeneity may stem from differences in experimental design and methodology as discussed in the following.

Experimentally targeting visuomotor comparisons

Manipulations of visuomotor congruence, and why their differences matter

Visual movement feedback can be manipulated to be incongruent with executed movements in several ways: One can show the participant an entirely different visual movement (e.g., the experimenter's), or one can displace (introducing spatial incongruence) or delayed (introducing temporal incongruence) the visual movement with respect to the participant's actual movement. Figure 3 shows examples of each kind of manipulation during a prototypical movement with continuous visual feedback (i.e., as during natural body movements). In

principle, the same ideas apply to discrete movement feedback e.g. in other experimental settings; however, it should be noted that (some) kinematics of visual movements might need to be inferred from discrete feedback, which would introduce another computational step.

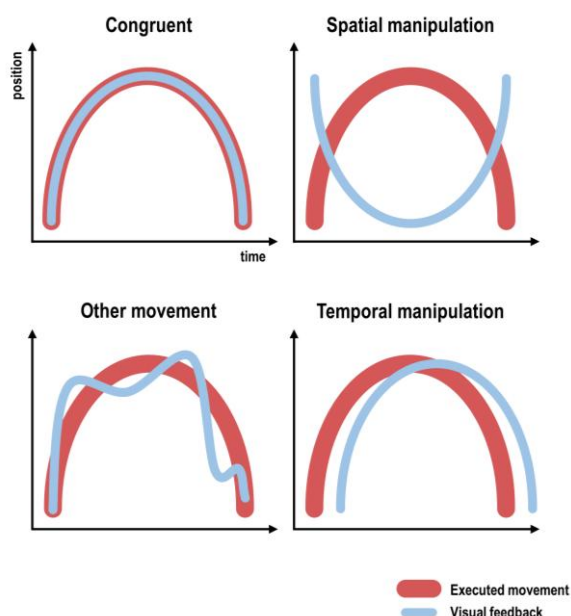


Figure 3: Common manipulations of (continuous) visual movement feedback for studying visuomotor self-other distinction. Shown is a schematic movement (where position changes along a single dimension, e.g. vertical displacement) with congruent feedback (top left); with spatially manipulated visual feedback (in this case, mirrored, top right); overlaid with another movement (bottom left); or with an added time delay (i.e., lagging, bottom right).

The idea to display another person's movements to a participant during execution dates back at least to Nielsen's (1963) "alien hand" experiment: His participants drew a line, while in some conditions seeing their own hand – in other conditions, they saw an image of the experimenter's hand, which occasionally made deviating line drawings. This principle has been adopted by many subsequent studies; which displayed different gestures or movements of different fingers during the participants' movements (e.g., Brass et al., 2009; Iacoboni et al., 2001; Kontaris et al., 2009; David et al. 2007). With the accessibility of MR compatible virtual reality technology, it is even possible to gradually morph self-generated movement signals with those of others, which opens up further interesting questions about the individual thresholds of visuomotor self-other distinction (see Yomogida et al. 2010; Nahab et al., 2011; Ohata et al. 2020, for examples). The common principle of studies using this kind of manipulation is that another person's movements cannot be predicted (to the same extent) by one's motor system; the observed movement should, therefore, result in an error response at the comparator that

can be used for self-other distinction. In contrast, distorted visual movement feedback can also be created from the participant's own movements; i.e., by shifting them in space or time. For instance, spatial displacement can be implemented via mirrors or prisms; temporal lag can be implemented by introducing delays to video recordings of the participant's movements or, more recently, to motion-captured movement data displayed through virtual hand models (Limanowski et al., 2017; Tanaka & Imamizu, 2025).

An excellent overview of visuomotor mismatch processing can be found in the reviews and meta-analyses by (Jeannerod, 2003; David et al., 2008; Sperdutti et al., 2011; Archambault et al., 2015; Zito et al., 2020; Seghezzi et al., 2021). To summarize those: Most studies reported extensive brain responses to mismatching visual feedback including two or more of the candidate regions (Fig. 2), among many others. Regions in and around the AG (with peak locations sometimes in the neighboring supramarginal gyrus, SMG) have been relatively consistently associated with detecting and processing visuomotor mismatches; including other movement-overlays (Farrer et al., 2008; Nahab et al., 2011; Ohata et al., 2020) and delays (van Kemenade et al., 2017, 2019; Balslev et al., 2006; Limanowski et al., 2017; Vigh & Limanowski, 2025). However, practically all of these studies have also reported qualitatively similar activation differences also in the LOTC (i.e., including putative EBA regions) and/or the STS. Some studies have specifically highlighted the STS (Leube et al., 2003, using delays; Kontaris et al., 2009, using other movement-overlays), whereas others have emphasized the EBA (David et al., 2007, 2009; Yomogida et al., 2010, using other movements), or their interplay processing different kinds of visual mismatches (Limanowski et al., 2017, using delays).

In sum, regarding the candidate visuomotor comparators shown in Fig. 2, the results are heterogeneous. The differences in experimental design between studies likely contributed to this. In particular, differences in the kind of executed movement and the degree of experimental control over it are particularly problematic when trying to disentangle visuomotor from visuo-proprioceptive comparisons. As shown schematically in Figure 3, each manipulation of visual

movement feedback (spatial, temporal, or overlay with another movement) implies a positional mismatch between executed and seen movements and, consequently, a mismatch of seen and felt body part positions. This means that, independently of the kind of visual manipulation, visual (e.g., EBA and STS, and potentially, AG) brain responses to the incongruence could be (partly or entirely) due to processing 'static' visuo-proprioceptive mismatches; i.e., frame-to-frame positional mismatches between seen and felt body positions.

The functional distinction between the candidate comparator areas could be improved by a systematic comparison of the errors (and their dynamics) resulting from the different kinds of feedback manipulation; especially spatial vs temporal manipulations (Box 1, cf. Peters et al., 2025). Partly based on the similar empirical (neuronal and behavioral) responses to spatial and temporal visuomotor mismatches, some authors have proposed their principled comparability regarding self-other distinction (Farrer et al., 2008b; Krugwasser et al., 2019). In contrast, Rohde and Ernst (2016) have, convincingly, argued that sensory feedback delays are a different kind of error signal than spatial errors (displacement), because they signal changes to action timing and initiation; which links them much more closely to (violations of) volition and agency (see also Tanaka & Imamizu, 2025, for a similar claim).

Relating to the functional specialization of the visual (biological) motion processing areas EBA and STS, one key distinction is that a constant spatial manipulation preserves the higher-order visual kinematics; i.e., the visual movement speed, acceleration, jerk, etc. always correspond to those of the actually executed movement. So, even though the moving body part's position in space, or its posture, may be altered (mirror flipped, for instance), the participant still controls the visual kinematics "on-line"; i.e., as during normal movements with veridical feedback. In contrast, a time delay will alter all visual kinematics; i.e., the visual (body part) position in space *as well as* its speed, acceleration, jerk etc. For instance, speeding up one's movement will not immediately result in an equally sped-up visual movement—vision will speed up only after the added delay, at a time when the executed movement speed may again have changed (exceptions are e.g. circular or sinusoidal movements with constant velocity, see Rohde &

Ernst, 2016). This has implications for how predictable the visual mismatches are initially. Thus, the “frame-by-frame” visual mismatch is harder to predict for delayed visual feedback, because the altered kinematics imply a nonlinear spatial transformation of position. In other words, the limb position and posture of delayed visual movements will not be predictable through an “easy” spatial transformation, as for displaced movement feedback. Therefore, one could expect larger error signals in the comparator(s) when processing delayed, compared with displaced visual movement feedback. An overlay with another visual movement entirely will potentially amplify this error response even further, as the visual mismatch over time is even less predictable. In the following section, I shall review approaches that try to capitalize on this kind of predictability; i.e., the fact that (some) errors can be learned by the motor system.

Prediction and learning of new visual movement feedback: Adaptation studies

A fundamental characteristic that distinguishes spatial *and* temporal distortions from overlays with entirely other movements (see above) is that the former two are, in principle, predictable from one’s motor signals. This means that the brain’s internal models can re-learn visuomotor associations and feedback control: Through an adaptation of the forward model’s predictions by sensory prediction errors (from the comparison of predicted and actual feedback, see Fig. 1A), one can learn to move under the novel visual movement feedback (Shadmehr et al., 2010; Krakauer & Mazzoni, 2011; cf. Ogawa et al., 2006, 2007; Grafton et al., 2008).

While a systematic analysis of temporal vs spatial adaptation is missing, visuomotor adaptation studies have highlighted the role of regions in the LOTC (i.e., potentially including the EBA) during the early adaptation phase (reviewed in Limanowski, 2022). The PPC is, among other regions, also implied in this learning; however, visuomotor adaptation seems to predominantly engage the superior parietal lobule. This could indicate a selectively augmented processing of novel visual movement feedback, likely in the dorsal network, for more efficient learning. Thus, the STS or AG seem not particularly involved in processing vision for adaptation itself.

Using continuous hand-target tracking tasks with variably delayed virtual hand movements, we could show that the SMG (near the AG) and the STS responded parametrically and continually

to the amount of visuomotor mismatch, while the LOTC (EBA) responded momentarily more strongly when novel visuomotor relationships were introduced (Limanowski et al., 2017; Vigh & Limanowski, 2025). This could hint at an “earlier” role of the EBA in processing unpredicted visual feedback. Furthermore, we found that the SMG’s responses to delays were slightly attenuated during adaptation, while cerebellar signals were elevated (Vigh & Limanowski, 2025). The cerebellar response profile is what one would expect from forward models (i.e., increased activity during delay suggesting computation of new predictions; cf. Kufer et al., 2024; Tzvi et al., 2022; Kiltner & Ehrsson, 2024), whereas the attenuation in the SMG is what one would expect of a “comparator” (i.e., reduced error signal after adaptation, because the visual feedback is now better predicted). Thus, in principle, adaptation designs could contribute to isolating visuomotor comparisons. However, as visuomotor adaptation may entail visuo-proprioceptive recalibration (Henriques & Cressmann, 2012; Block et al., 2013; Limanowski, 2022; Kufer et al., 2024), lower ‘mismatch responses’ following adaptation could also result from recalibrated sensation rather than adapted forward predictions.

Here, it is worth investigating differences between spatial vs temporal manipulations of visual movement feedback; i.e., the corresponding adaptation process. Recall that spatial manipulations preserve the timing of visual kinematics (see above). This means that any visually conveyed movement error (i.e., a mismatch between desired and actual visual movement consequences) can be used to adjust control just as during ‘normal’ action—requiring only an additional transformation of (visual) coordinates in space. This allows for efficient feedback control and visuomotor adaptation. Based on the assumption that in feedback control systems like the brain’s, the forward model entails a prediction of sensory delays (potentially, a “Smith predictor”, Foulkes & Miall, 2000; Miall et al., 1993, see above), the delay predictions of internal models could be re-learned as well. Thus, although delay adaptation has received comparably less attention from researchers than spatial adaptation (but see the excellent synthesis by Rohde & Ernst, 2016), it has received some experimental support (Foulkes & Miall, 2000; Botzer & Karniel, 2013; Perrinet et al., 2014). Correspondingly, Wen (2019) concluded that participants may indeed experience control during visual delays. It

should, however, be noted that delay adaptation likely has limits—particularly for goal-directed movements with complex movement trajectories (Perrinet et al., 2014). The main reason for this is that the time between the actual execution of an “error” and a potential error correction, i.e., a correction of the motor commands through adjusted forward sensory predictions (see above), increases with the delay. In other words, error correction will become increasingly more “off-line” under large delays, which renders feedback control much more ineffective or even impossible (Foulkes & Miall, 2000; Leib et al., 2024).

The key difference to spatial displacements is that for delay adaptation, the delay component of the forward model, not its predictions of position, needs updating. Delays could thereby be a more domain general quantity or ‘agency’ error signal (Rohde & Ernst, 2016). A resulting empirical (neuroanatomical) question is whether sensory feedback delays are also registered by different comparators than spatial manipulations—and whether appropriately designed studies could thus contribute to identifying the loci of visuomotor comparators (Box 1).

Manipulations of visual movement feedback during passive vs active movements

Brain responses to visuomotor self-other distinction can be isolated through the combined (factorial) manipulation of visual feedback congruence and the locus of movement generation; i.e., active, self-generated vs passive, externally generated. Passive (externally induced) body movements of the participant generate identical visual and proprioceptive feedback as active movements, but lack the respective motor predictions. The resulting interaction effect should isolate brain responses specifically related to the visuomotor comparison process: A brain region responding more strongly (or even exclusively) to mismatching visual movement feedback during active, compared with passive movements (Fig. 1A). A similar logic has been applied in the somatosensory domain, starting with the seminal experiments by Blakemore et al. (1998; cf. Weiskrantz et al., 1971). However, only a handful of brain imaging studies have used such “interaction” designs in the visuomotor domain:

Christensen and colleagues (2007a) compared active (self-generated) vs passive ankle movements, with or without visual movement feedback conveyed by a cursor drawing a curve reflecting a goniometer signal from the foot. The passive movements were implemented by an experimenter moving the foot. Passive > active movements were associated with increased BOLD signal in the bilateral TPJ (including regions around the AG and STS), alongside many other brain areas, including the medial and superior frontal cortex and bilateral sensorimotor cortices. The interaction effect – looking at stronger activation increases to visual feedback > no vision during passive relative to active movements – revealed significant effects near the bilateral STS, the anterior temporal cortex, and medial, superior, and inferior frontal cortices.

Taking an analogous approach in fMRI study, *Limanowski, Sarasso et al. (2018)* had participants perform right-hand rotations actively, or those rotations were generated by the experimenter (i.e., passive movements); in each case with or without visual feedback of the moving hand. Here, the movement feedback was conveyed by a photorealistic 3D virtual hand model via motion-tracking. Passive, compared with active movements overall increased activity in the bilateral STS (alongside further activations in parietal and superior frontal cortices). There was a significant interaction effect between visual feedback and agency in the right posterior STS: its response to visual movement feedback > no feedback was significantly increased during passive, compared with active movements. This suggested that the right STS evaluated visuo-motor mismatches.

Other studies have added temporal delays to the visual action feedback. In an fMRI study by *Balslev and colleagues (2006)*, participants moved a sliding mouse with their finger, or the experimenter moved their finger analogously; while participants viewed movement feedback via a cursor, which moved synchronously or asynchronously (here, the viewed movement was a play-back of previous trials, which was either leading or lagging the actual movement). FMRI scanning revealed increased activation in the right AG by asynchronous compared with synchronous feedback during both active and passive movements. There was no significant interaction effect; i.e., no differential processing of incongruence depending on agency. The

authors concluded that the observed AG activation was, therefore, indicative of visuo-proprioceptive, rather than visuo-motor comparisons.

In a study by *Tsakiris and colleagues (2010)*, participants lifter their index finger – or the experimenter lifted it – while viewing camera captured videos of the finger movement; which could be synchronous (with an intrinsic delay of 100 ms) or asynchronous (delayed by 500 ms). The fMRI analysis showed several clusters of activation related to the main effect of asynchronous > synchronous visual feedback, which included bilateral temporo-parietal regions around the AG. Furthermore, the main effect of passive > active movements was reflected by relatively stronger activation of several brain areas, including the bilateral STS alongside medial and superior frontal areas, the precuneus, the cingulate gyrus, and the bilateral postcentral gyrus. No interaction effects were reported. Based on the slightly (but non-significantly) different activation profiles of several regions around the right TPJ, the authors speculated that some of them (around the AG) may register visuo-proprioceptive conflicts, while others, in the more superior SMG, may play a role in visuomotor comparisons and agency attribution.

Another group of researchers has used elegant pneumatic setups allowing the generation of passive (vs active) hand movements inside the MR scanner, to investigate the agency dependent processing of visual movement feedback. Thus, in *van Kemenade et al. (2018)*, participants either performed active hand movements, or passive hand movements were executed via the pneumatic device; while participants viewed camera recordings of their hand, which were delayed by variable amounts. In this study, the authors focused their analysis on BOLD signal correlations with the *amount of delay* in each condition; i.e., on the interaction effect of agency with delay. The respective main effects (differences between conditions) were subsequently reported in *Arikan et al. (2019)*: Passive > active movements were, on average, associated with stronger activity in a wide spread network of brain areas. Thereby, the strongest effects and largest clusters obtained from this contrast were located in the bilateral STS. Similarly, the amount of visual delay was positively correlated with activity in the right

LOC and the bilateral STS; however, without significant differences between active and passive conditions in these areas (such a difference was found in the right cerebellum). Based on the absence of an interaction effect (i.e., of differences in delay correlation between active and passive movement conditions), the authors concluded that activity in these areas more likely reflects general visuo-proprioceptive conflict detection than an agency specific i.e., visuomotor process. In a variation of this design, *Uhlmann et al. (2020)* looked at active vs passive movements (under delayed visual feedback) while also manipulating the visual hand identity to be “self” or “other”. The fMRI results revealed an overall increased activity in the bilateral STS, alongside further frontal, parietal, and cerebellar activations, during passive > active trials; and, moreover, stronger STS and hippocampal activity during trials in which the seen hand identity was “other” > “self”. An interaction effect was found in the bilateral AG, the bilateral superior frontal cortex, the precuneus, and the middle temporal gyrus; i.e., in these regions, activity was increased during passive > active movements when one's own hand > someone else's hand was seen. This suggests that forward models may incorporate visual hand identity into their predictions.

In sum, the anticipated interaction effect was not coherently observed in the reviewed studies. The only coherent finding across the reviewed studies was the increased STS (and, in some studies, AG) activation by observed visual movement feedback generated by passive, compared with active movements. This result is consistent with work in monkeys (Hietanen & Perrett, 1996) and with the previous observation that the STS responds more strongly to observation of others' movements (see above). Activity increases in the IPL/STS can also be found in passive > active movements without any visual feedback (Limanowski et al., 2020; cf. Jaeger et al., 2014); which could indicate such STS responses reflecting differences in “passivity” (task disengagement). Possibly, the STS responses could also encode social aspects of the experiment such as interactions with the experimenter guiding the passive movement (but several studies found these responses using automated induction of passive movements, e.g., Uhlmann et al., 2020; Limanowski et al., 2020).

Nevertheless, these kinds of interaction designs should be pursued to isolate visuomotor from visuoproprioceptive comparisons in the brain. One potential reason for the inconsistent effects in the above studies are methodological problems associated with the very challenging implementation of “truly passive” movements. Pushing or pulling body parts generates all kinds of somatosensation (on the skin, in the joints etc.). Participants might notice this especially at the movement onset, and move “cooperatively”. Future work could explore the use of functional electrical muscle stimulation to induce passive movements; i.e., through stimulation of the same muscles (cf. Iftime-Nielsen et al., 2012; Limanowski et al., 2020). Another potential modification of the above designs is depriving the participants of proprioceptive feedback; which can be done by using ischemic nerve block or anesthetics (e.g., Christensen et al., 2007b). The absence of proprioceptive information would make an interpretation of brain activity increases during incongruent visual movements in terms of mere visuo-proprioceptive comparison unlikely. These experiments could be linked to neuropsychological findings in deafferented (i.e., with a partial or complete lack of proprioceptive afferent) patients; i.e., these patients can adapt to distorted visual movement feedback, but may be unaware of the underlying learning and recalibration process (e.g., Fournier et al., 2002; Farrer et al., 2003; Miall & Cole, 2007). While there are still many controversies about what kind of afferent signals can be received by these patients (Miall & Cole, 2007), neuropsychological case studies open up a unique perspective on which comparison processes are truly fundamental for motor control and/or the conscious access to the underlying computations (cf. Jeannerod, 1986; Wolpert et al., 1998; Sirigu et al., 1999). Finally, the induction of passive (vs active) movements can be combined with visuomotor adaptation tasks. From a computational perspective, which focuses on learning through updates of the motor system’s forward model (see above), action should be necessary for adaptation. Indeed, there is substantial evidence that sensorimotor adaptation is impaired during passive movements (Lackner, 1977; cf. Henriques & Cressmann, 2012; Rohde & Ernst, 2016; Kufer et al., 2024). Thus, any significant interaction effects in the resulting cortical adaptation could, in principle, be interpreted as indicating visuomotor comparisons during action, specifically.

Conclusion

In the past years, many important insights have been gained into the neurocomputational architecture underlying the self-other distinction based on visual and action cues. Thereby the forward/comparator model framework has proven valuable for hypothesis generation and for the design of brain imaging studies testing these hypotheses. There is considerable support for an implication of the AG, EBA, and STS in self-other distinction based on visual and action cues. While the question whether the “action cues” received by those regions are motor or non-motor cannot yet conclusively be answered (among other questions, Box 1), there are promising methodological developments suggesting that, in principle, it can be.

Box 1: Key open questions

- **Where is the visuomotor comparator – if there is a single one?**

Some of the reviewed evidence suggests supramodal comparisons in e.g. the AG, while other studies suggest specific comparisons in the EBA or the STS; i.e., regions specialized in visual body/motion perception. Models of biological motion processing or social cognition imply a serial communication of the EBA and the STS (e.g. Giese & Poggio, 2003), EBA and the AG (Jeannerod, 2004), and of the AG/TPJ and the STS (e.g. Patel et al., 2019). This could be reconciled within a hierarchical process of self-other distinction, in which these regions communicate with each other. An interesting question is whether there are specialized comparator “modules” or, rather, gradients (cf. Beauchamp et al., 2002; Lingnau & Downing, 2015) in self-other distinction as well.

- **Do ventral visual areas receive motor signals—and do they implement comparators or forward models?**

Visual processing in the EBA or STS may be biased by action cues, but whether these regions receive motor signals such as the efference copy has not yet been demonstrated clearly enough. Functional and structural connectivity studies in humans should identify potential afferents from motor regions; e.g., those supposedly implementing forward models. Furthermore, regions in the LOTC encode parameters of upcoming actions, which could imply a role closer to a forward model (Gallivan & Culham, 2015; cf. Zimmermann et al., 2016, 2018; Quirnbach & Limanowski, 2024). Ventral visual areas could thus themselves compute the forward predictions based on motor signals, rather than receiving those predictions and comparing them against sensory reafference. This could (but need not) mean that visuomotor evaluations are reserved for other brain areas like the cerebellum or the PPC (cf. Blakemore et al., 1998; MacDonald and Paus, 2003).

- **Does hemodynamic activity in comparator modules (only) reflect mismatches?**

The common assumption reviewed here is that comparators can be identified through their increased (hemodynamic) responses to mismatching action feedback, reflecting population responses to sensorimotor prediction errors evoked by unpredicted movement feedback. However, “sharpening” accounts propose a selective augmentation of neuronal responses tuned to predicted (self-generated) action feedback (Yon et al., 2018). This could mean that comparators show more complex, contextual activity profiles; and that experiments should account for this (Press et al., 2020).

- **What is the contribution of spatial vs temporal cues to visually based self-other distinction?**

Different kinds of visual distortions imply differences in kinematic predictability and, potentially, control and learning—all of which could influence visuomotor evaluations in the candidate comparator areas. A comparison of the sensitivity to, and the—potentially separate or hierarchical—processing of spatial vs temporal distortions is necessary. This can be addressed by designs systematically combining more than kind of manipulation in appropriate time-resolved designs.

- **How can we achieve better experimental control over non-motoric cues?**

Purely sensory cues, such as proprioception and its congruence with vision, can also be used to ascribe observed movements to oneself or another. To isolate motor comparators, new methods of generating truly passive movements via e.g. muscle stimulation are needed. These could be combined with adaptation designs, which offer another angle at locating motor predictions; or with the addition of noise, or temporary attenuation of proprioception. This research would contribute to answering the related question whether or not there are sensorimotor comparators that ignore intersensory congruence.

Acknowledgments

This work was supported by a Freigeist Fellowship of the VolkswagenStiftung (AZ 97-932).

The brain render was generated with SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/>).

References

- Adams, R. A., Shipp, S., & Friston, K. J. (2013). Predictions not commands: active inference in the motor system. *Brain Structure and Function*, 218, 611-643.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in cognitive sciences*, 4(7), 267-278.
- Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual review of neuroscience*, 25(1), 189-220.
- Apps, M. A. J., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. *Neuroscience & Biobehavioral Reviews*, 41, 85–97.
<https://doi.org/10.1016/j.neubiorev.2013.01.029>
- Archambault, P. S., Ferrari-Toniolo, S., Caminiti, R., & Battaglia-Mayer, A. (2015). Visually-guided correction of hand reaching movements: The neurophysiological bases in the cerebral cortex. *Vision research*, 110, 244-256.
- Arikan, B. E., van Kemenade, B. M., Podranski, K., Steinsträter, O., Straube, B., & Kircher, T. (2019). Perceiving your hand moving: BOLD suppression in sensory cortices and the role of the cerebellum in the detection of feedback delays. *Journal of Vision*, 19(14), 4-4.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature neuroscience*, 7(5), 542-548.
- Azim, E., & Seki, K. (2019). Gain control in the sensorimotor system. *Current opinion in physiology*, 8, 177-187.
- Bahrack, L. E., & Watson, J. S. (1985). Detection of intermodal proprioceptive–visual contingency as a potential basis of self-perception in infancy. *Developmental psychology*, 21(6), 963.
- Balslev, D., Nielsen, F. Å., Lund, T. E., Law, I., & Paulson, O. B. (2006). Similar brain networks for detecting visuo-motor and visuo-proprioceptive synchrony. *Neuroimage*, 31(1), 308-312.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, 34(1), 149-159.
- Bermúdez, J. L. (2001). Nonconceptual self-consciousness and cognitive science. *Synthese*, 129, 129-149.
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, 1(7), 635-640.
- Blakemore, S. J., & Sirigu, A. (2003). Action prediction in the cerebellum and in the parietal lobe. *Experimental Brain Research*, 153, 239-245.

- Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, 88(1), 145–166. <https://doi.org/10.1016/j.neuron.2015.09.029>
- Block, H., Bastian, A., & Celnik, P. (2013). Virtual lesion of angular gyrus disrupts the relationship between visuoproprioceptive weighting and realignment. *Journal of cognitive neuroscience*, 25(4), 636-648.
- Botzer, L., & Karniel, A. (2013). Feedback and feedforward adaptation to visuomotor delay during reaching and slicing movements. *European Journal of Neuroscience*, 38(1), 2108-2123.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2359-2367.
- Brown, H., Adams, R. A., Parees, I., Edwards, M., & Friston, K. (2013). Active inference, sensory attenuation and illusions. *Cognitive processing*, 14, 411-427.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*, 50(3), 1148-1167.
- Christensen, M. S., Lundbye-Jensen, J., Petersen, N., Geertsen, S. S., Paulson, O. B., & Nielsen, J. B. (2007a). Watching your foot move—An fMRI study of visuomotor interactions during foot movement. *Cerebral Cortex*, 17(8), 1906-1917.
- Christensen, M. S., Lundbye-Jensen, J., Geertsen, S. S., Petersen, T. H., Paulson, O. B., & Nielsen, J. B. (2007b). Premotor cortex modulates somatosensory cortex during voluntary movements without proprioceptive feedback. *Nature neuroscience*, 10(4), 417-419.
- Cieslik, E. C., Mueller, V. I., Eickhoff, C. R., Langner, R., & Eickhoff, S. B. (2015). Three key regions for supervisory attentional control: Evidence from neuroimaging meta-analyses. *Neuroscience & Biobehavioral Reviews*, 48, 22–34. <https://doi.org/10.1016/j.neubiorev.2014.11.003>
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron*, 58(3), 306–324. <https://doi.org/10.1016/j.neuron.2008.04.017>
- Dasgupta, S., Tyler, S. C., Wicks, J., Srinivasan, R., & Grossman, E. D. (2017). Network connectivity of the right STS in three social perception localizers. *Journal of Cognitive Neuroscience*, 29(2), 221-234.
- David, N., Cohen, M. X., Newen, A., Bewernick, B. H., Shah, N. J., Fink, G. R., & Vogeley, K. (2007). The extrastriate cortex distinguishes between the consequences of one's own and others' behavior. *Neuroimage*, 36(3), 1004-1014.
- David, N., Newen, A., & Vogeley, K. (2008). The “sense of agency” and its underlying cognitive and neural mechanisms. *Consciousness and cognition*, 17(2), 523-534.

- De Vignemont, F., & Fournieret, P. (2004). The sense of agency: A philosophical and empirical review of the "Who" system. *Consciousness and cognition*, 13(1), 1-19.
- Decety, J., Chaminade, T., Grèzes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage*, 15(1), 265-272.
- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The neuroscientist*, 13(6), 580-593.
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, 4, 423-431.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470-2473.
- Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, 305(5685), 875-877.
- Erickson, L. C., Rauschecker, J. P., & Turkeltaub, P. E. (2017). Meta-analytic connectivity modeling of the human superior temporal sulcus. *Brain Structure and Function*, 222(1), 267-285.
- Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *Neuroimage*, 15(3), 596-603.
- Farrer, C., Franck, N., Georgieff, N., Frith, C., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: A positron emission tomography study. *NeuroImage*, 18(2), 324-333.
- Farrer, C., Franck, N., Paillard, J., & Jeannerod, M. (2003). The role of proprioception in action recognition. *Consciousness and cognition*, 12(4), 609-619.
- Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S., & Grafton, S. T. (2008). The angular gyrus computes action awareness representations. *Cerebral Cortex*, 18(2), 254-261, <https://doi.org/10.1093/cercor/bhm050>.
- Farrer, C., Bouchereau, M., Jeannerod, M., & Franck, N. (2008b). Effect of distorted visual feedback on the sense of agency. *Behavioural Neurology*, 19(1-2), 53-57.
- Foulkes, A. J. M., & Miall, R. C. (2000). Adaptation to visual feedback delays in a human manual tracking task. *Experimental brain research*, 131, 101-110.
- Fournieret, P., Paillard, J., Lamarre, Y., Cole, J., & Jeannerod, M. (2002). Lack of conscious recognition of one's own actions in a haptically deafferented patient. *Neuroreport*, 13(4), 541-547.
- Friston, K., Mattout, J., & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics*, 104(1), 137-160.
- Frith, C. D., & Frith, U. (1999). Interacting minds--a biological basis. *Science*, 286(5445), 1692-1695.

- Frith, C. D., Blakemore, S. J., & Wolpert, D. M. (2000). Explaining the symptoms of schizophrenia: abnormalities in the awareness of action. *Brain Research Reviews*, 31(2-3), 357-363.
- Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in cognitive sciences*, 4(1), 14-21.
- Gallese, V., & Sinigaglia, C. (2010). The bodily self as power for action. *Neuropsychologia*, 48(3), 746–755. <https://doi.org/10.1016/j.neuropsychologia.2009.09.038>
- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, 4(3), 179-192.
- Giese, M. A. Biological and Body Motion Perception. IN Wagemans, J. (Ed.). (2015). *The Oxford handbook of perceptual organization*. OUP Oxford.
- Grafton, S. T., Schmitt, P., Van Horn, J., & Diedrichsen, J. (2008). Neural substrates of visuomotor learning based on improved feedback control and prediction. *Neuroimage*, 39(3), 1383-1395.
- Graziano, M. S. A., & Botvinick, M. M. (1999). How the brain represents the body: Insights from neurophysiology and psychology. In D. Gopher, & A. Koriath (Eds.), *Attention and performance XVII—Cognitive regulation of performance interaction of theory and application* (pp. 136–157)
- Grezes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions?. *Neuroimage*, 13(5), 775-785.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of cognitive neuroscience*, 12(5), 711-720.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35(6), 1167-1175.
- Grünbaum, T., & Christensen, M. S. (Eds.) (2017). *Sensation of Movement*. Abingdon, UK: Routledge. (Current Issues in Consciousness Research).
- Grünbaum, T., & Christensen, M. S. (2020). Measures of agency. *Neuroscience of consciousness*, 2020(1), niaa019.
- Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, 18(4), 196-207.
- Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34(2-3), 102-254.
- Henriques, D. & Cressman, E. (2012) Visuomotor Adaptation and Proprioceptive Recalibration. *Journal of Motor Behavior*, 44(6), 435-444.
- Hietanen, J. K., & Perrett, D. I. (1996). Motion sensitive cells in the macaque superior temporal polysensory area: response discrimination between self-generated and externally generated pattern motion. *Behavioural brain research*, 76(1-2), 155-167.

- Hirai, M., & Senju, A. (2020). The two-process theory of biological motion processing. *Neuroscience & Biobehavioral Reviews*, 111, 114-124.
- Humphreys, G. F., & Tibon, R. (2023). Dual-axes of functional organisation across lateral parietal cortex: the angular gyrus forms part of a multi-modal buffering system. *Brain Structure and Function*, 228(1), 341-352.
- Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., ... & Rizzolatti, G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the national academy of sciences*, 98(24), 13995-13999.
- Iftime-Nielsen, S. D., Christensen, M. S., Vingborg, R. J., Sinkjær, T., Roepstorff, A., & Grey, M. J. (2012). Interaction of electrical stimulation and voluntary hand movement in SII and the cerebellum during simulated therapeutic functional electrical stimulation in healthy adults. *Human Brain Mapping*, 33(1), 40-49.
- Jaeger, L., Marchal-Crespo, L., Wolf, P., Riener, R., Michels, L., & Kollias, S. (2014). Brain activation associated with active and passive lower limb stepping. *Frontiers in Human Neuroscience*, 8, 828.
- Jastorff, J., & Orban, G. A. (2009). Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing. *Journal of Neuroscience*, 29(22), 7315-7329.
- Jeannerod, M. (1986). Mechanisms of visuomotor coordination: a study in normal and brain-damaged subjects. *Neuropsychologia*, 24(1), 41-78.
- Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural brain research*, 142(1-2), 1-15.
- Jeannerod, M. (2004). Visual and action cues contribute to the self–other distinction. *Nature neuroscience*, 7(5), 422-423.
- Jeannerod, M. (2006). *Motor cognition: What actions tell the self* (No. 42). Oxford University Press.
- Johnson, J. F., Belyk, M., Schwartz, M., Pinheiro, A. P., & Kotz, S. A. (2019). The role of the cerebellum in adaptation: ALE meta-analyses on sensory feedback error. *Human brain mapping*, 40(13), 3966-3981.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Processing*, 8, 159-166.
- Kilteni, K., & Ehrsson, H. H. (2024). Dynamic changes in somatosensory and cerebellar activity mediate temporal recalibration of self-touch. *Communications Biology*, 7(1), 522.
<https://doi.org/10.1038/s42003-024-06188-4>

- Kontaris, I., Wiggett, A. J., & Downing, P. E. (2009). Dissociation of extrastriate body and biological-motion selective areas by manipulation of visual-motor congruency. *Neuropsychologia*, 47(14), 3118-3124.
- Krakauer, J. W., & Mazzoni, P. (2011). Human sensorimotor learning: adaptation, skill, and beyond. *Current opinion in neurobiology*, 21(4), 636-644.
- Krugwasser, A. R., Harel, E. V., & Salomon, R. (2019). The boundaries of the self: The sense of agency across different sensorimotor aspects. *Journal of Vision*, 19(4), 14-14.
- Kufer, K., Schmitter, C. V., Kircher, T., & Straube, B. (2024). Temporal recalibration in response to delayed visual feedback of active versus passive actions: An fMRI study. *Scientific Reports*, 14(1), 4632. <https://doi.org/10.1038/s41598-024-54660-2>
- Lackner, J. R. (1977). Adaptation to visual and proprioceptive rearrangement: origin of the differential effectiveness of active and passive movements. *Perception & Psychophysics*, 21(1), 55-59.
- Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *Journal of Neuroscience*, 26(11), 2894-2906.
- Leib, R., Howard, I. S., Millard, M., & Franklin, D. W. (2024). Behavioral motor performance. *Comprehensive Physiology*, 14(1), 5179-5224.
- Leube, D. T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. (2003). The neural correlates of perceiving one's own movements. *Neuroimage*, 20(4), 2084-2090.
- Limanowski, J. (2021). Precision control for a flexible body representation. *Neuroscience & Biobehavioral Reviews*.
- Limanowski, J., & Blankenburg, F. (2013). Minimal self-models and the free energy principle. *Frontiers in Human Neuroscience*, 7. <https://doi.org/10.3389/fnhum.2013.00547>
- Limanowski, J., Lutti, A., & Blankenburg, F. (2014). The extrastriate body area is involved in illusory limb ownership. *NeuroImage*, 86, 514–524. <https://doi.org/10.1016/j.neuroimage.2013.10.035>
- Limanowski, J., & Blankenburg, F. (2016). Integration of Visual and Proprioceptive Limb Position Information in Human Posterior Parietal, Premotor, and Extrastriate Cortex. *The Journal of Neuroscience*, 36(9), 2582–2589. <https://doi.org/10.1523/JNEUROSCI.3987-15.2016>
- Limanowski, J., Kirilina, E., & Blankenburg, F. (2017). Neuronal correlates of continuous manual tracking under varying visual movement feedback in a virtual reality environment. *NeuroImage*, 146, 81–89. <https://doi.org/10.1016/j.neuroimage.2016.11.009>
- Limanowski, J., & Blankenburg, F. (2017). Posterior parietal cortex evaluates visuoproprioceptive congruence based on brief visual information. *Scientific Reports*, 7(1), 16659.
- Limanowski, J., Sarasso, P., & Blankenburg, F. (2018). Different responses of the right superior temporal sulcus to visual movement feedback during self-generated vs. externally generated hand movements. *European Journal of Neuroscience*, 47(4), 314-320.

- Limanowski, J., Lopes, P., Keck, J., Baudisch, P., Friston, K., & Blankenburg, F. (2020). Action-dependent processing of touch in the human parietal operculum and posterior insula. *Cerebral Cortex*, 30(2), 607-617.
- Lingnau, A., & Downing, P. E. (2015). The lateral occipitotemporal cortex in action. *Trends in cognitive sciences*, 19(5), 268-277.
- Luppino, G., Calzavara, R., Rozzi, S., & Matelli, M. (2001). Projections from the superior temporal sulcus to the agranular frontal cortex in the macaque. *European Journal of Neuroscience*, 14(6), 1035-1040.
- MacDonald, P. A., & Paus, T. (2003). The role of parietal cortex in awareness of self-generated movements: a transcranial magnetic stimulation study. *Cerebral Cortex*, 13(9), 962-967.
- Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: dummy hands and peripersonal space. *Behavioural brain research*, 191(1), 1-10.
- Mars, R. B., Sallet, J., Schüffegen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. (2012). Connectivity-based subdivisions of the human right “temporoparietal junction area”: evidence for different areas participating in different cortical networks. *Cerebral cortex*, 22(8), 1894-1903.
- Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport*, 14(17), 2135-2137.
- Miall, R. C., & Jackson, J. K. (2006). Adaptation to visual feedback delays in manual tracking: evidence against the Smith Predictor model of human visually guided action. *Experimental Brain Research*, 172(1), 77-84.
- Miall, R. C., & Cole, J. (2007). Evidence for stronger visuo-motor than visuo-proprioceptive conflict during mirror drawing performed by a deafferented subject and control subjects. *Experimental Brain Research*, 176(3), 432-439.
- Miall, R. C., Weir, D. J., Wolpert, D. M., & Stein, J. F. (1993). Is the Cerebellum a Smith Predictor? *Journal of Motor Behavior*, 25(3), 203–216. <https://doi.org/10.1080/00222895.1993.9942050>
- Moayed, M., Noroozbahari, N., Hadjis, G., Themelis, K., Salomons, T. V., Newport, R., & S Lewis, J. (2021). The structural and functional connectivity neural underpinnings of body image. *Human brain mapping*, 42(11), 3608-3619.
- Molenberghs, P., Brander, C., Mattingley, J. B., & Cunnington, R. (2010). The role of the superior temporal sulcus and the mirror neuron system in imitation. *Human Brain Mapping*, 31(9), 1316-1326.
- Moore, J. W., & Fletcher, P. C. (2012). Sense of agency in health and disease: a review of cue integration approaches. *Consciousness and cognition*, 21(1), 59-68.
- Nahab, F. B., Kundu, P., Gallea, C., Kakareka, J., Pursley, R., Pohida, T., ... & Hallett, M. (2011). The neural processes underlying self-agency. *Cerebral cortex*, 21(1), 48-55.

- Nielsen, T. I. (1963). Volition: A new experimental approach. *Scandinavian journal of psychology*, 4(1), 225-230.
- Ogawa, K., Inui, T., & Sugio, T. (2006). Separating brain regions involved in internally guided and visual feedback control of moving effectors: An event-related fMRI study. *NeuroImage*, 32(4), 1760–1770. <https://doi.org/10.1016/j.neuroimage.2006.05.012>
- Ogawa, K., Inui, T., & Sugio, T. (2007). Neural Correlates of State Estimation in Visually Guided Movements: An Event-Related FMRI Study. *Cortex*, 43(3), 289–300. [https://doi.org/10.1016/S0010-9452\(08\)70455-6](https://doi.org/10.1016/S0010-9452(08)70455-6)
- Ohata, R., Asai, T., Kadota, H., Shigemasu, H., Ogawa, K., & Imamizu, H. (2020). Sense of agency beyond sensorimotor process: decoding self-other action attribution in the human brain. *Cerebral Cortex*, 30(7), 4076-4091.
- Paillard, J. (1999). Body Schema and body image-a double dissociation. *Motor control, today and tomorrow*, 197, 214.
- Palmer, C. E., Davare, M., & Kilner, J. M. (2016). Physiological and perceptual sensory attenuation have different underlying neurophysiological correlates. *Journal of neuroscience*, 36(42), 10803-10812.
- Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews Neuroscience*, 3(8), 606-616.
- Patel, G. H., Sestieri, C., & Corbetta, M. (2019). The evolution of the temporoparietal junction and posterior superior temporal sulcus. *Cortex*, 118, 38-50.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, 49(6), 815-822.
- Perrett, D. I., Smith, P. A. J., Mistlin, A. J., Chitty, A. J., Head, A. S., Potter, D. D., ... & Jeeves, M. A. (1985). Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: a preliminary report. *Behavioural brain research*, 16(2-3), 153-170.
- Perrinet, L. U., Adams, R. A., & Friston, K. J. (2014). Active inference, eye movements and oculomotor delays. *Biological cybernetics*, 108, 777-801.
- Peters, F., Wang, P., & Limanowski, J. (2025). Action enhances the detection of visuomotor incongruence: A comparison of matched spatial vs temporal manipulations along identical trajectories. *bioRxiv*, 2025-06.
- Petit, L., Ali, K. M., Rheault, F., Boré, A., Cremona, S., Corsini, F., ... & Sarubbo, S. (2023). The structural connectivity of the human angular gyrus as revealed by microdissection and diffusion tractography. *Brain Structure and Function*, 228(1), 103-120.
- Peuskens, H., Vanrie, J., Verfaillie, K., & Orban, G. A. (2005). Specificity of regions processing biological motion. *European Journal of Neuroscience*, 21(10), 2864-2875.

- Pitcher, D., & Ungerleider, L. G. (2021). Evidence for a third visual pathway specialized for social perception. *Trends in Cognitive Sciences*, 25(2), 100-110.
- Press, C., Kok, P., & Yon, D. (2020). The perceptual prediction paradox. *Trends in cognitive sciences*, 24(1), 13-24.
- Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358(1431), 435-445.
- Quirnbach, F., & Limanowski, J. (2024). Visuomotor prediction during action planning in the human frontoparietal cortex and cerebellum. *Cerebral Cortex*, 34(9), bhae382.
<https://doi.org/10.1093/cercor/bhae382>
- Reznik, D., & Mukamel, R. (2019). Motor output, neural states and auditory perception. *Neuroscience & Biobehavioral Reviews*, 96, 116-126.
- Rockland, K. S. (2023). Angular gyrus: an anatomical case study for association cortex. *Brain Structure and Function*, 228(1), 131-143.
- Rohde, M., & Ernst, M. O. (2016). Time, agency, and sensory feedback delays during action. *Current Opinion in Behavioral Sciences*, 8, 193-199.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature reviews neuroscience*, 11(4), 264-274.
- Salomon, R., Lim, M., Kannape, O., Llobera, J., & Blanke, O. (2013). "Self pop-out": agency enhances self-recognition in visual search. *Experimental brain research*, 228(2), 173-181.
- Schmitter, C. V., Pazen, M., Uhlmann, L., van Kemenade, B. M., Kircher, T., & Straube, B. (2025). Predictive neural processing of self-generated hand and tool actions in patients with schizophrenia spectrum disorders and healthy individuals. *Translational Psychiatry*, 15(1), 85.
- Scott, S. H. (2012). The computational and neural basis of voluntary motor control and planning. *Trends in cognitive sciences*, 16(11), 541-549.
- Scott, S. H., Cluff, T., Lowrey, C. R., & Takei, T. (2015). Feedback control during voluntary motor actions. *Current opinion in neurobiology*, 33, 85-94.
- Seghezzi, S., Convertino, L., & Zapparoli, L. (2021). Sense of agency disturbances in movement disorders: A comprehensive review. *Consciousness and cognition*, 96, 103228.
- Seltzer, B., & Pandya, D. N. (1989). Frontal lobe connections of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology*, 281(1), 97-113.
- Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual review of neuroscience*, 33(1), 89-108.

- Sirigu, A., Daprati, E., Pradat-Diehl, P., Franck, N., & Jeannerod, M. (1999). Perception of self-generated movement following left parietal lesion. *Brain*, 122(10), 1867-1874.
- Sperduti, M., Delaveau, P., Fossati, P., & Nadel, J. (2011). Different brain structures related to self-and external-agency attribution: a brief review and meta-analysis. *Brain Structure and Function*, 216(2), 151-157.
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of comparative and physiological psychology*, 43(6), 482.
- Stenner, M. P., Bauer, M., Heinze, H. J., Haggard, P., & Dolan, R. J. (2015). Parallel processing streams for motor output and sensory prediction during action preparation. *Journal of neurophysiology*, 113(6), 1752-1762.
- Synofzik, M., Vosgerau, G., & Newen, A. (2008a). Beyond the comparator model: a multifactorial two-step account of agency. *Consciousness and cognition*, 17(1), 219-239.
- Synofzik M, Vosgerau G, Newen A. (2008b) I move, therefore I am: a new theoretical framework to investigate agency and ownership. *Consciousness and Cognition*, 17(2):411-424.
doi:10.1016/j.concog.2008.03.008
- Synofzik, M., Thier, P., Leube, D. T., Schlotterbeck, P., & Lindner, A. (2010). Misattributions of agency in schizophrenia are based on imprecise predictions about the sensory consequences of one's actions. *Brain*, 133(1), 262-271.
- Tanaka, T., & Imamizu, H. (2025). Sense of agency for a new motor skill emerges via the formation of a structural internal model. *Communications Psychology*, 3(1), 70.
- Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia*, 48(3), 703-712.
- Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body: neural signatures of agency and body-ownership. *Neuropsychologia*, 48(9), 2740-2749.
- Tsakiris, M., Haggard, P., Franck, N., Mainy, N., & Sirigu, A. (2005). A specific role for efferent information in self-recognition. *Cognition*, 96(3), 215-231.
- Tzvi, E., Loens, S., & Donchin, O. (2022). Mini-review: The Role of the Cerebellum in Visuomotor Adaptation. *The Cerebellum*, 21(2), 306–313. <https://doi.org/10.1007/s12311-021-01281-4>
- Uddin, L. Q., Supekar, K., Amin, H., Rykhlevskaia, E., Nguyen, D. A., Greicius, M. D., & Menon, V. (2010). Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cerebral cortex*, 20(11), 2636-2646.
- Uhlmann, L., Pazen, M., van Kemenade, B. M., Steinsträter, O., Harris, L. R., Kircher, T., & Straube, B. (2020). Seeing your own or someone else's hand moving in accordance with your action: The neural interaction of agency and hand identity. *Human brain mapping*, 41(9), 2474-2489.

- Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences*, 98(20), 11656-11661.
- van Kemenade, B. M., Arian, B. E., Kircher, T., & Straube, B. (2017). The angular gyrus is a supramodal comparator area in action–outcome monitoring. *Brain Structure and Function*, 222(8), 3691-3703.
- van Kemenade, B. M., Arian, B. E., Podranski, K., Steinsträter, O., Kircher, T., & Straube, B. (2019). Distinct roles for the cerebellum, angular gyrus, and middle temporal gyrus in action–feedback monitoring. *Cerebral Cortex*, 29(4), 1520-1531.
- Vangeneugden, J., Peelen, M. V., Tadin, D., & Battelli, L. (2014). Distinct neural mechanisms for body form and body motion discriminations. *Journal of Neuroscience*, 34(2), 574-585.
- von Holst, E., Mittelstaedt, H. (1950). Das Reafferenzprinzip. *Naturwissenschaft* 37 (37), 464–476.
- Vigh, G., & Limanowski, J. (2025). That's (relevant for) me: Task set dependent brain responses to delayed visual movement feedback. *Social Cognitive And Affective Neuroscience*, nsaf097.
- Villa, R., Ponsi, G., Scattolin, M., Panasiti, M. S., & Aglioti, S. M. (2022). Social, affective, and non-motoric bodily cues to the Sense of Agency: A systematic review of the experience of control. *Neuroscience & Biobehavioral Reviews*, 142, 104900.
- Weiskrantz, L., Elliott, J., & Darlington, C. (1971). Preliminary observations on tickling oneself. *Nature*, 230(5296), 598-599.
- Wen, W. (2019). Does delay in feedback diminish sense of agency? A review. *Consciousness and cognition*, 73, 102759.
- Wolpert, D.M., Miall, R.C., 1996. Forward models for physiological motor control. *Neural Networks*, 9, 1265–1279.
- Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations: the role of the human superior parietal lobe. *Nature neuroscience*, 1(6), 529-533.
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, 11(18), R729–R732. [https://doi.org/10.1016/S0960-9822\(01\)00432-8](https://doi.org/10.1016/S0960-9822(01)00432-8)
- Yakar, F., Çeltikçi, P., Doğruel, Y., Egemen, E., & Güngör, A. (2023). The connectivity-based parcellation of the angular gyrus: Fiber dissection and MR tractography study. *Brain Structure and Function*, 228(1), 121-130.
- Yeterian, E. H., & Pandya, D. N. (1991). Corticothalamic connections of the superior temporal sulcus in rhesus monkeys. *Experimental Brain Research*, 83(2), 268-284.
- Yomogida, Y., Sugiura, M., Sassa, Y., Wakusawa, K., Sekiguchi, A., Fukushima, A., Takeuchi, H., Horie, K., Sato, S., & Kawashima, R. (2010). The neural basis of agency: An fMRI study. *NeuroImage*, 50(1), 198–207. <https://doi.org/10.1016/j.neuroimage.2009.12.054>

- Yon, D., Gilbert, S. J., de Lange, F. P., & Press, C. (2018). Action sharpens sensory representations of expected outcomes. *Nature communications*, 9(1), 4288.
- Zimmermann, M., Verhagen, L., de Lange, F. P., & Toni, I. (2016). The extrastriate body area computes desired goal states during action planning. *Eneuro*, 3(2).
- Zimmermann, M., Mars, R. B., De Lange, F. P., Toni, I., & Verhagen, L. (2018). Is the extrastriate body area part of the dorsal visuomotor stream?. *Brain Structure and Function*, 223(1), 31-46.
- Zito, G. A., Wiest, R., & Aybek, S. (2020). Neural correlates of sense of agency in motor control: A neuroimaging meta-analysis. *PLoS One*, 15(6), e0234321.