

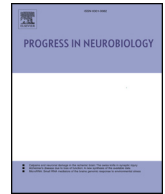
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State estimation in posterior parietal cortex: Distinct poles of environmental and bodily states

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ABSTRACT

Posterior parietal cortex (PPC) has been implicated in sensory and motor processing, but its underlying organization is still debated. Sensory-based accounts suggest that PPC is mainly involved in attentional selection and multisensory integration, serving novelty detection and information seeking. Motor-specific accounts suggest a parietal subdivision into lower-dimensional, effector-specific subspaces for planning motor action. More recently, function-based interpretations have been put forward based on coordinated responses across multiple effectors evoked by circumscribed PPC regions. In this review, we posit that an overarching interpretation of PPC's functional organization must integrate, rather than contrast, these various accounts of PPC. We propose that PPC's main role is that of a state estimator that extends into two poles: a rostral, body-related pole that projects the environment onto the body and a caudal, environment-related pole that projects the body into an environment landscape. The combined topology interweaves perceptual, motor, and function-specific principles, and suggests that actions are specified by top-down guided optimization of body-environment interactions.

1. Current ideas about the driving forces of posterior parietal cortical organization

Posterior parietal cortex (PPC) is usually described as a sensorimotor interface, acknowledging two dominant functional roles: to merge information from multiple senses such as vision, audition, and touch, and to plan and execute actions based on transformations of this sensory input. However, the underlying function of PPC, as well as the factors driving its large-scale organization, are still hotly debated (Caminiti et al., 2010; Fattori et al., 2017; Galletti and Fattori, 2018; Huntenburg et al., 2018; Mars et al., 2018, 2011; Vallar and Coslett, 2018; Xu, 2018). Although serial accounts of cognitive function have long proven inadequate, and the inseparability of sensory and motor processing is now widely acknowledged, many research programmes have pitted the “sensory” and “motor” in “sensorimotor” against each other. Accordingly, different research directions have scrutinized PPC organization each with a particular set of questions in mind. Interpretation of experimental results is restricted by the applied manipulations and controls (Krakauer et al., 2017), often emerging as quasi consensus within a (sub-)field.

Here, we promote rethinking PPC organization with the notion that sensory and motor function are inseparable, and that an overarching account of PPC organization must take on a perspective that embraces their interaction. We propose that PPC is best understood when viewed from an angle that accentuates estimating the state of the body relative to the environment and, vice versa, the state of the environment relative to the body. This view embraces the integrative, sensorimotor role of PPC (Gottlieb, 2007; Gottlieb and Balan, 2010; Siegel et al., 2015; Snyder, 2000a), its role of continually defining the best next action, and of supervising its execution in a sensorimotor control loop (Cisek and Kalaska, 2010; Pezzulo and Cisek, 2016).

Our proposal focuses on the dorsal surface of PPC, and its comparable areas in the macaque monkey and human (see Fig. 1c), mostly excluding the medial surface of PPC within the medial longitudinal fissure that separates the two hemispheres. This latter region is made up of the precuneus, a region whose function has been thought to relate to representation of the self, but that may also be involved in providing a stable internal model of an individual's own body in the environment (Land, 2014; Peer et al., 2015). It may, therefore, principally be possible to include this region into the scheme we develop here, and we

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will offer some thoughts about this possibility in the outlook at the end of the paper. Note, precuneus extends onto the dorsal PPC surface, and we refer to the medial-most surface region when we mention this structure elsewhere.

1.1. Sensory-based accounts of PPC organization

Sensory-based accounts suggest that PPC is mainly involved in attentional selection (Bisley and Mirpour, 2019). Resting state data and neuroimaging studies have suggested that PPC houses two attentional networks, with dorsal PPC areas, including the SPL, involved in top-down attentional orienting, and ventral regions, including the temporoparietal junction (TPJ), involved in bottom-up attentional orienting (Corbetta and Shulman, 2002; Shomstein et al., 2012). These systems may serve the detection of novelty, guiding curiosity-driven behavior, and aiding information seeking (Gottlieb et al., 2013).

Fitting a sensory-based notion, PPC displays a rostral-to-caudal organizational gradient from somatosensory to visual dominance, as one might expect given the locations of the respective primary sensory regions. For example, area 5 in the rostral portion of PPC (Fig. 1c) features a somatosensory homunculus similar to its neighboring primary somatosensory cortex (Penfield and Boldrey, 1937; Roux et al., 2018), with notable magnification of the body parts that are most relevant to a given species (Seelke et al., 2011; Taoka et al., 1998). Slightly more caudal, monkey ventral intraparietal area (VIP), and an analogous region in humans, contain head-centered tactile maps that overlap, or are interspersed with, visual maps for looming stimuli (Cléry et al., 2017; Guipponi et al., 2013; Huang et al., 2012; Sereno and Huang, 2014). The same portion of PPC also processes sensory inputs related to heading direction, such as visual flow and vestibular signals (Chen et al., 2013; Drugowitsch et al., 2014; Fetsch et al., 2013), further stressing its role in multisensory integration. Similarly, visual responses related to an individual's own arm have been reported in area 5 (Graziano et al., 2000), and a cytoarchitecturally defined region of area 5 at the dorsocaudal pole of the medial PPC, termed PEC (Pandya and Seltzer, 1982) exhibits visual and somatosensory responses to hand and foot (Bakola et al., 2010; Breveglieri et al., 2008). These latter responses are likely related to limb position and complex postures (Bakola et al., 2010; Piserchia et al., 2017), possibly during self-movement (Serra et al., 2019). Neurons of a region situated more posteriorly between primary somatosensory and visual cortices, area V6A, usually respond to visual stimulation, but about 30% of its neurons exhibit tactile or proprioceptive responses, especially related to the arm (Breviglieri et al., 2008; Fattori et al., 2017; Gamberini et al., 2011). The very selective coding of the arms, but not other body parts, and neuronal coding of hand orientation and formation, suggest a role in object-related reaching (Fattori et al., 2017). Finally, research with a focus on the organization of visual processing has suggested that multiple visual maps extend from occipital cortex all the way to anterior PPC, referred to as IPSO-5 in humans (Fig. 1c, right), presumably reflecting higher cognitive functionality the further anterior are located (Szczepanski et al., 2013), and the more they integrate visual signals with other sensory signals (Rohe and Noppeney, 2016).

1.2. Effector-based accounts of PPC organization

Strict sensory-based accounts of PPC organization are challenged by findings that suggest local specialization related to movement of specific effectors (Andersen and Cui, 2009; Grefkes and Fink, 2005; Kastner et al., 2017; Snyder, 2000b; Vesia and Crawford, 2012). Numerous electrophysiological studies in non-human primates have suggested that the lateral intraparietal area (LIP) encodes eye movement plans, whereas the parietal reach region (PRR), which contains the medial intraparietal area (MIP) and area V6A, is responsive to impending reaches (Andersen and Cui, 2009; Bosco et al., 2016). Likewise, transcranial magnetic stimulation (TMS) over human PPC can cause

selective impairments of saccade and reach planning (Vesia et al., 2010a, 2010b). Human fMRI studies have shown that PPC contains multiple maps specific to saccades hand pointing, or hand reach direction (IPSO-5, see Fig. 1c, right panel) (Gallivan et al., 2011; Hagler et al., 2007; Kastner et al., 2017; Konen and Kastner, 2008; Leoné et al., 2014b). When participants plan movements towards the location opposite to an instructional cue, PPC initially codes sensory information, but motor-related information thereafter (Gail and Andersen, 2006; Medendorp et al., 2005; Zhang and Barash, 2000). PPC also represents the task rule, that is whether movements are to be directed towards or away from the cue (Connolly et al., 2000; Fernandez-Ruiz et al., 2007; Gail and Andersen, 2006; Klaes et al., 2011). These findings are at odds with a purely perceptual-attentional account of PPC and implicate a role in mediating sensorimotor transformations.

Extending this work, several human fMRI studies have suggested a rostral-to-caudal gradient for limb movements vs. saccades as one organizing principle of PPC (Beurze et al., 2009; Burnod et al., 1999; Caminiti et al., 2010; Heed et al., 2011, 2016b). This gradient may seem intuitive with respect to the rostral-to-caudal gradient relating to touch vs. vision, with vision and saccadic movements both occupying caudal regions. Note, however, that this match is by no means self-evident, since both hand reaches and saccades can obviously be made to both visual and tactile targets. Thus, the observed gradient seems to depend on the consequences that result from the respective type of movement: saccades have predominately visual consequences; limb movements have predominately proprioceptive and tactile consequences, and will often require further motor commands, for instance when correcting the trajectory of the moved limb, or to adjust other body parts to regain balance.

1.3. Challenges for an effector-specific account of PPC organization

1.3.1. Incomplete separation of eye and hand processing

The notion of effector specificity has led to the view that, in analogy to the somatotopic organization of primary somatosensory cortex, PPC is subdivided into lower-dimensional, effector-specific subspaces which define the current movement goal in relation to a specific effector (Andersen and Cui, 2009). Yet, in monkeys, both LIP and PRR also house neurons that are responsive to the non-preferred effector (Oristaglio et al., 2006; Snyder et al., 2000, 1997), and many human fMRI studies have emphasized considerable activation overlap in areas active for eye and hand movements (Gallivan et al., 2011; Hagler et al., 2007; Hinkley et al., 2009). Moreover, not all PPC regions fit easily into an effector-based scheme. For example, VIP houses neurons with visual, tactile, and auditory receptive fields (RFs) around the animal's body, while its motor role is associated with defensive movements involving a diversity of body parts, such as flinching, fletching the teeth, turning the head, and hiding the arm (Graziano and Cooke, 2006). Similar observations were made in the anterior intraparietal area (AIP) (Zhang et al., 2017); this area was traditionally believed to code for hand shape and grasping, but was recently reported to carry also signals related to both hands as well the shoulder in humans (Menz et al., 2015).

With the widely applied comparison of hand and eye movements, experiments supporting effector-based accounts have heavily relied on functionally vastly different systems. Whereas fingers and hands interact with the environment, the eyes serve perceptual rather than manipulative functions and are tightly linked to attentional processing (Corbetta et al., 1998). Also from a kinematics perspective, the spatial transformations needed to direct the hand to a visual target are entirely different than those required for eye movements (Crawford et al., 2011). Thus, ultimately neither differences nor similarities between eye and hand movements offer a complete picture about the large-scale organization of the parietal cortex.

Some studies have compared movements of the two arms (Beurze et al., 2007; Calton et al., 2002; Chang et al., 2008; Gallivan et al., 2013; Haar et al., 2017; Medendorp et al., 2005; Valyear and Frey,

2015). However, this approach suffers from the drawback that each arm is primarily controlled by the contralateral hemisphere, so that any differences in processing of the two limbs may be due to body symmetry rather than effector specificity.

1.3.2. Different effectors, similar parietal cortical activity

Like the hand, the foot can manipulate objects; and comparing activity for the limbs of one body side allows comparing effector-specific organization within one hemisphere. Currently, monkey data about goal-directed foot movements are not available. However, using fMRI, we have addressed the topic of large-scale organization of human PPC with a goal-directed pointing task with right hand, right foot, and the eyes.

In a first study, we observed a caudo-rostral gradient from eye to limb movement planning, but no segregation between foot and hand movement planning along the IPS (Heed et al., 2011). Only in rostral parts of PPC, adjacent to S1, there was a coarse, lateral-to-medial gradient for hand vs. foot planning, with overlapping hand and foot activation between more effector-specific activation swaths. Consistent with this result, others have shown that rhythmic ankle, finger, and elbow movements elicit largely overlapping fMRI activation along medial IPS, whereas effector-specific activation was evident in rostral PPC, laterally for the finger and medially for the ankle (Cunningham et al., 2013).

Using multivariate, multi-voxel pattern analysis of a completely new participant sample of the goal-directed pointing task, we confirmed the limb generality of caudal PPC regions, and further suggested that many of the more rostral regions distinguished one from the other two effectors (Leoné et al., 2014a): regions that responded predominately for one effector also held a common representation for the other two effectors. Together, these studies challenge a strict effector-specify view of PPC.

While multivariate approaches decode information across voxels in a region, they cannot distinguish the fine-grained neural organization within a given fMRI voxel: For regions that are active for several effectors, is movement planning for each respective effector mediated by separate neurons, or by a common neuron pool? fMRI repetition suppression (RS) approaches interpret BOLD signal reductions from one trial to the next as an indicator of overlapping neuron pools across trials (Grill-Spector and Malach, 2001; Valyear et al., 2012; Van Pelt et al., 2010). In an RS version of the hand, foot, and eye pointing task (Heed et al., 2016b), RS patterns suggested that a common neuronal pool mediates planning for all three effectors in caudal PPC, though with a bias for saccades in putative human LIP (Grefkes and Fink, 2005; Kastner et al., 2017). In rostral PPC, most regions showed RS patterns consistent with neuronal selectivity for either hand (laterally) or foot (medially), with the exception of one region between hand and foot regions whose neurons showed RS for both limbs, but not the eyes (Heed et al., 2016b). This activity pattern is generally consistent with segregated neuronal responses in area 5 of monkeys (Taoka et al., 2000, 1998), but notably also with a monkey region in rostral PPC responding to both limbs (Bakola et al., 2010; Breveglieri et al., 2008).

1.4. Functional aspects of PPC organization

1.4.1. Functionally determined activation during observation and imagery

The MRI environment places strong constraints on paradigms that involve overt movement. However, many motor regions exhibit activity not only when participants plan movements, but also when they either observe another individual making movements on video (Abdollahi et al., 2013; Cattaneo and Rizzolatti, 2009; Filimon et al., 2007; Hardwick et al., 2018), or when they imagine, rather than actually perform, motor actions (Bakker et al., 2008; Filimon et al., 2007; Hardwick et al., 2018; Lorey et al., 2014; Vingerhoets, 2014). Action observation and motor imagery studies can, therefore, be informative about the neural organization of PPC (Aflalo et al., 2015; Klaes et al.,

2015). When observers saw video clips of four different motor actions – dragging, dropping, grasping, and pushing – performed with either hand, foot, or mouth, PPC activation clustered according to the type of action, regardless of the employed effector (Jastorff et al., 2010). Consistent with this observation, the excitability of the primary hand motor area was enhanced by observing actions typically performed by the hand, even when those actions were performed with the foot; conversely, the excitability of the primary foot motor area was enhanced by viewing a typical foot action, independent of the effector actually being used in the observed (Senna et al., 2014). Another study compared observation of manipulation, locomotion and climbing (Abdollahi et al., 2013). Because climbing involves the same effectors as hand manipulation and locomotion combined, the authors reasoned that similar activations should be evident if PPC were organized in an effector-specific manner. However, the three action categories activated distinct regions in PPC, inconsistent with an effector-specificity account, and more consistent with a functional organization of PPC. Findings of imagery studies further support the conclusions of movement planning and movement observation studies. Although some differences were observed in a direct comparison of observation and imagery, activation with both kinds of paradigm showed stronger differences for different types of actions than for different effectors (Lorey et al., 2014).

In sum, common organizational principles of PPC emerge across versatile experimental approaches ranging from self-performed simple pointing and flexion movements to observation and imagination of complex whole-body movement. They do not prominently feature effector specificity as a major source of regional specialization within PPC; instead, they promote the importance of functional criteria, such as categories of actions.

1.4.2. Ecologically relevant action classes revealed by cortical stimulation

Electrical stimulation and optical imaging of PPC in several primate species have suggested that different regions of PPC, each connected to specialized premotor regions, mediate distinct functional classes of ecologically relevant movements, such as hand-to-mouth feeding, reaching, coordinated movements with all four limbs, and self-defense (Stepniewska et al., 2005, 2011; Baldwin et al., 2016; Graziano, 2016; Graziano and Aflalo, 2007). Like the human fMRI work, these results argue against an organization that represents individual effectors, and instead suggest that specialized regions elicit control of all effectors relevant for the respective movement class. This concept of action representation implies that the PPC is organized to initiate several classes of ethologically relevant behaviors, based on sensory and intrinsic signals, and mediated via connections of PPC with premotor and motor cortex (Mars et al., 2018, 2011; Orban, 2016; Stepniewska et al., 2011). This organization has probably developed in parallel with the phylogenetic emergence of increasingly sophisticated motor functions across mammalian species that addressed complex demands of specialized interaction with the environment (Caminiti et al., 2015; Cisek, 2019). Reaching and grasping movements, for example, are thought to have evolved from the neural systems that served to actively position the limb during locomotion (Georgopoulos and Grillner, 1989; Karl and Whishaw, 2013). This common ancestral notion may also explain why behavioral writing characteristics are rather invariant to the effectors used, being it the hand, mouth or foot (Rijntjes et al., 1999) or that people born without hands can learn to use the feet as hands.

In addition, many typical actions involve the coordination of multiple effectors. Regional overlap for different effectors, therefore, appears instrumental for resolving the challenge that many redundant actions could solve a given task. This notion is in line with previous suggestions that entertaining separate machinery for coding similar planned movements that only differ in the effector used to execute them is computationally inefficient (Levy et al., 2007). In fact, single neuron activity in the anterior intraparietal area of a tetraplegic patient has been reported to code many variables, including body part, body side,

and task characteristics, within the same neuronal population (Zhang et al., 2017). However, although the neuronal population coded for all tested body parts, neural coding was independent between them. This type of mixed neural coding (Fusi et al., 2016) could be at the heart of an effector-overarching, functional organization.

2. Towards an integrated view of PPC: Optimal Feedback Control

The different accounts of PPC organization – perception vs. action, somatosensory vs. visual processing, effectors vs. action classes – demonstrate that the proposed lawful solutions to the underdetermined, multidimensional problem of organizing PPC into a two-dimensional neuronal matrix much depend on the focus of the research question and the involved task paradigms. Viewed this way, depending on how one cuts through the hyperspace of solutions implemented by the PPC, each specific account could serve as a governing principle, perhaps to support the whole brain for achieving optimal performance. The traditional approach of contrasting perceptual with action-related, motor function has led to seemingly incompatible solutions to the PPC puzzle. We posit that understanding the overarching functional organization of PPC will require integrating, rather than contrasting, these views of brain function. In serving this overall goal, optimal feedback control (OFC) theory (Todorov, 2004), which is a prominent theory in motor control, suggests that sensation and movement are merely inseparable aspects of an action control loop. The theory shares some commonalities with current theories about active inference and predictive coding (Friston, 2011, 2010). OFC can shed new light on the debate about the role of the PPC: rather than segregating sensory and motor roles, it suggests to inquire about the overarching purpose and principles of sensorimotor integration.

In the OFC framework (Fig. 1a), the brain must continually estimate both the state of the environment and the state of the body and combine the two to elicit and control adequate behavior. In this process of state estimation, the brain integrates sensory input with predictions of

sensory inputs based on outputs of internal forward models, which represent the mapping between motor commands and sensory consequences (Oostwoud Wijdenes and Medendorp, 2017; Scott, 2012; Shadmehr and Krakauer, 2008). There is indeed evidence that PPC activity predicts the sensory consequences of upcoming movements (Mulliken et al., 2008; Pilacinski et al., 2018; Sirigu et al., 1996) as well as sensorimotor prediction errors during motor learning (Savoie et al., 2018). Moreover, PPC activity predicts future eye position (Dowiasch et al., 2016).

Here, we extend this view and propose that it is possible to subsume the discussed organizational principles of PPC under a common roof of state estimation. In particular, we suggest that state estimation organizes the PPC into a rostral, body-related pole, and a caudal, environment-related pole (Fig. 1b). Thus, while in OFC models and its simulations, the various state variables are represented by a single state vector that is estimated and updated when the movement unfolds and/or the environment changes (Diedrichsen et al., 2010; Schwartz, 2016; Shadmehr and Krakauer, 2008), we propose that this vector is cortically mapped along the rostral-to-caudal axis of PPC layout.

2.1. A rostral-to-caudal gradient for state estimation: body vs. environment

In our framework, caudal PPC represents an environmental landscape and projects the body in relation to that landscape, so that it can be associated with other objects in the environment. This function explains the predominance of visual, or more generally external-spatial, processing, with vision providing information of even far distant objects and events for which current body posture is of no or little relevance. Furthermore, for objects and events near the body, caudal PPC relates non-visual to visual information to code the body relative to the environment. This is in line with the well-documented dominance of eye-centered spatial coding in caudal PPC, that is, the modulation of neuronal activity by the distance of visual targets or acting effectors from the line of gaze (Batista et al., 1999; Cui, 2014; Medendorp et al.,

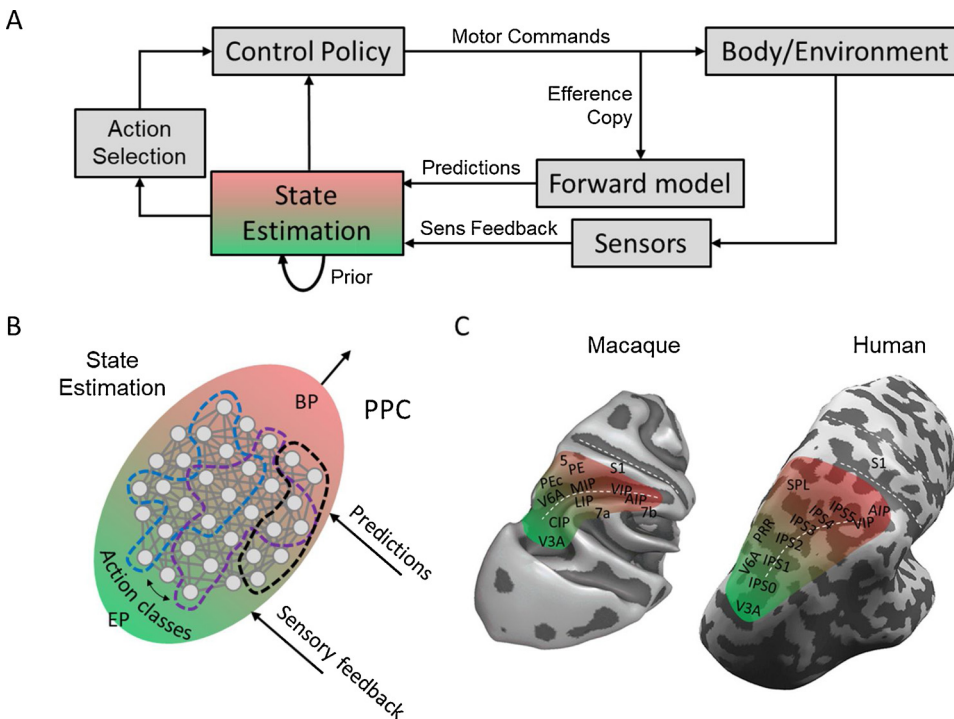


Fig. 1. Illustration of optimal feedback control theory and its possible large-scale implementation in the brain. A. Optimal Feedback Control (figure based on Shadmehr and Krakauer, 2008). The state estimator combines current sensory information with the predicted outcomes based on motor outputs (through an internal forward model) as well as information about the expected sensory state (the prior), accumulated over comparable circumstances. A process of action selection specifies the goal of the behavior, based on action-clustered inputs of the state estimator. The control policy reflects a set of rules, including feedback gains, specifying how to act given the estimated current state of the body and world to perform the action. B. State estimation in PPC extends into a body-related (BP) and an environment-related pole (EP) along the rostral-caudal dimension. The medial-to-lateral gradient is dominated by action classes, involving interconnected neuronal networks, often involving the same units (see blue, purple and black dashed-tracings). C. Comparison of monkey and human PPC. Dashed lines indicate the central sulcus and the intraparietal sulcus (IPS), which divides the superior parietal (SPL) and inferior parietal lobule (IPL). Regions are shown on semi-inflated cortical surfaces, to also indicate regions in the bank of the IPS. In both species, the red-to-green gradient illustrates the rostral-to-caudal gradient for state estimation from a body-related to an environment-related pole. Monkey PPC contains regions such as Brodmann's areas 5, 7A and 7B; PEc and PE; visual areas V3A and V6A; and CIP, LIP, MIP, AIP, and VIP, as located along the IPS. Human PPC contains many of the same regions, as well as additional, topographic areas IPS0-5 located along the IPS. PRR is functionally defined; it overlaps MIP and V6A. For meanings of the abbreviations that name different brain regions, see main text.

2003). Moreover, spatial information is predictively updated across eye movements to maintain a stable, allocentric representation in this reference frame (Duhamel et al., 1992; Mirpour and Bisley, 2016). Finally, caudal PPC activity reflects the expected visual consequences of planned movements, suggesting that planning is initially based on body-independent specification of the intended action effects (Pilacinski et al., 2018). Note, however, that the preference for eye-centered coding is relative, rather than absolute (Bosco et al., 2016; Hadjidimitrakis et al., 2014; McGuire and Sabes, 2011; Pesaran et al., 2006). Thus, in caudal PPC, this reference frame is used not only to code visual information, but also body-related information such as hand position (Batista et al., 1999; Beurze et al., 2007; Hadjidimitrakis et al., 2014; Medendorp et al., 2005).

Behavioral and imaging work on tactile localization support this notion; this research area has addressed the division into body-related and environment-related representation. For instance, identifying a limb can be error prone, and humans can confuse tactile stimuli between the two hands and even between a hand or a foot (Badde et al., 2019; Schicke and Röder, 2006; Shore et al., 2002; Yamamoto and Kitazawa, 2001). Also, tactile stimuli to the right hand appear to be coded as “left” – thus, in external, presumably gaze-centered space (Heed et al., 2016a) – in the environment-related pole of PPC when the hand is crossed over to the left side of space (Ruzzoli and Soto-Faraco, 2014) or when the stimulated, right-hand finger is placed left of gaze (Buchholz et al., 2013, 2011). TMS to caudal PPC disrupts the computation of this tactile external location (Azañón et al., 2010; Bolognini and Maravita, 2007). Together, these findings suggest that caudal PPC “projects” the body into the environment.

Next, our framework suggests an opposite, complementary role for rostral PPC: this region estimates the state of the body, that is, the configuration of the body and its parts, and funnels relevant, environmental information onto the body. The core function of body processing is reflected in the predominance of sensory information that is unique to the body, that is, touch, proprioception, and vestibulation. However, rostral PPC furthermore relates other sensory information, such as vision and audition, to the body, so that it codes the environment relative to the body. Accordingly, body and body-part centered reference frames dominate neural coding in rostral regions (Bremner and Andersen, 2012; Chen et al., 2013; Schlack et al., 2005; Sereno and Huang, 2006), coding environmental events with respect to that body part’s current position (Heed et al., 2015). For instance, VIP neurons appear to code visual stimuli relative to their tactile receptive field (Duhamel et al., 1998; Graziano and Cooke, 2006). Thus, rostral PPC recodes, or maps, sensory information onto the body in a format that is highly compatible with the coding requirements for motor action and sensorimotor control loops. The proposed role of rostral PPC in body state estimation is consistent with studies that have observed fMRI activation related to body posture in rostral PPC, both in the context of sensorimotor tasks (Parkinson et al., 2010; Pellijeff et al., 2006) as well as during observation of hand actions (Zimmermann et al., 2013). Likewise, it is supported by the report about a patient who, after a lesion located presumably in SPL, lost the ability to keep track of her arm’s postural state (Wolpert et al., 1998).

In effect, both rostral and caudal PPC serve the same underlying function, namely, to relate body and environment, but the two poles employ opposite perspectives. A rostral-to-caudal gradient for state estimation in PPC is in line with multiple studies that contrast the two poles of PPC. In the context of reach planning, caudal region PRR uses predominately eye-centered coding, whereas rostral region 5d employs hand-centered coding (Beurze et al., 2010; Bremner and Andersen, 2012; Buneo et al., 2002). In fact, temporal evolution from representing the hand relative to the eye before, and the target relative to the hand after, reach target presentation has been suggested to reflect the process of state estimation for the hand during reach planning (Bremner and Andersen, 2014), in line with our proposed scheme. Furthermore, monkeys with PPC lesions located in rostral areas 5, 7b, and MIP are

unable to reach in the dark, that is, when they have to rely on proprioceptive information (Rushworth et al., 1997); in contrast, they perform successfully in the light, that is, when they can rely on visual information alone. The opposite behavioral pattern is observed in monkeys with lesions in caudal PPC areas LIP and 7a, suggesting that they cannot relate their movements to visual information. Similarly, prism-induced reaching errors relating to the hand movement evoked adaptive neuronal activity in monkey area 5, whereas errors relating to the reach target evoked adaptive activity in area 7 (Inoue and Kitazawa, 2018).

The PPC gradient for state estimation also accommodates the observed processing during movement planning with different limbs. Common activity in caudal PPC, independent of whether the participant will move eyes, hand, or foot, suggests that stimulus evaluation proceeds disregarding its concrete realization by a particular body movement (Heed et al., 2016b). Limb-specific coding, evident only in rostral PPC, may be realized by routing limb-unspecific information from caudal PPC to limb-specific, rostral regions (Heed et al., 2016b, 2011).

Our framework potentially accommodates various observations that can follow damage to parietal cortex, such as optic ataxia and neglect. For instance, patients suffering from optic ataxia after bilateral lesions close to the environmental pole were impaired in gaze-centered updating of reach targets (Khan et al., 2005b, 2005a). In addition, the relative influence of hand and target position in optic ataxia reportedly depended on the location of the lesion relative to the environmental vs. body pole in patients with unilateral lesions (Khan et al., 2013, 2007), consistent with our framework. Finally, spatial neglect, a disorder in which patients ignore events and objects on one (usually the left) side, can occur in multiple forms. Some patients neglect tactile information, others visual information, and it is of note that there is a form of tactile-visual extinction – the neglect of a left-sided tactile stimulus when a right-sided visual stimulus is present at the same time – that depends on the visual stimulus being located in peripersonal space that is, in the space in which tactile and visual spaces come together (Ládavas et al., 1998). We note, however, that we are not aware that these different forms of neglect have been associated with a particular parietal gradient regarding the underlying brain damage.

Tool use, too, integrates conceptually with our framework. We regard tool use as a special case in which the environment must be projected onto the body: the state of the tool is tightly linked to the state of the body in terms of sensorimotor processing (Miller et al., 2018). Conversely, the state of the body-and-tool must be projected into the environment, as is the case in planning any other goal-directed activity. For instance, activation in caudal PPC areas was found to be different for naming tools compared to animals, perhaps a task that requires environmental projection, whereas in more anterior PPC the activation differed for grasping and reaching to the tool, that is, when the tool must be projected onto the body (Valyear et al., 2007). Other studies, too, have observed two distinct parietal areas for tool use, one related to movement planning more in the putative environmental pole, and the one for the actual movement execution in the body pole (Johnson-Frey et al., 2005).

2.2. A medial-to-lateral gradient for action classes

We have, so far, concentrated on only one dimension – from rostral to caudal – of the posterior parietal cortical sheet. We suspect that the second dimension, a medial-to-lateral gradient, is dominated by action classes. The homuncular organization of the primary motor and premotor cortex has been radically reinterpreted based on the occurrence of functionally distinct movements that can involve multiple limbs (Stepniewska et al., 2005; Graziano and Aflalo, 2007; Graziano, 2016). Computational modelling has suggested that the organization of premotor regions may emerge as the layout that minimizes projections for each effector (Graziano and Aflalo, 2007). Although comparable

modeling work has not been performed for PPC, the distribution of regions mediating observation of multi-limb movements in humans and multi-limb movements in other species is conceptually compatible with a similar, map-like organization also in this brain region.

Such a use-dependent concept inherently explains the relatively larger size of cortical areas dedicated to extensively used limbs, such as the hand in humans, as compared to those for less important limbs, in the progression from S1 to adjacent, more caudal regions (Krubitzer, 2007). Already in S1, limbs that play an important role in the animal's behavior cover larger parts of cortex than other body parts (Krubitzer, 2007). Area 5 in SPL exhibits a strong bias for the hand, but also contains neurons responsible for the feet; the overall medial-to-lateral organization follows that of S1 (Breviglieri et al., 2008; Taoka et al., 2000). In IPS, the AIP with finger and hand selectivity is located most laterally, whereas the arm reaching-related MIP is located more medially. Results from both action observation and reaching studies have suggested some hand and foot overlap in the SPL region between the more distant lateral hand and medial foot poles (Abdollahi et al., 2013; Cunningham et al., 2013; Heed et al., 2016b, 2011). Note, the dominance of body-related criteria for the organization of cortical regions is well in line with the rostral-to-caudal body-environment gradient we propose. This topology makes the PPC very suited as a system that both selects and coordinates effectors, rather than representing, in each sub-region, one specific effector. PPC organization is less obvious in more caudal regions but appears to be dominated by functional aspects related to the interaction with the environment (Fattori et al., 2017), again consistent with our rostral-to-caudal gradient.

Separately from these considerations that are based on body layout and action classes, a functional segregation in the medio-lateral direction has also been proposed from the perspective of visuomotor processing. Posterior parietal cortex is the target of the dorsal visual stream – a pathway that was originally broadly implicated in spatial vision (Ungerleider and Mishkin, 1982) and in vision for action (Goodale and Milner, 1992). Yet, subsequent accounts have suggested that the dorsal pathway is in fact formed by two streams, a dorsal-dorsal stream that processes vision for action, and a dorsal-ventral stream that processes space and action perception (Rizzolatti and Matelli, 2003), later further specified a dorso-dorsal Grasp system with a role in prehensile actions, and a Use system for skilled functional object use (Binkofski and Buxbaum, 2013). Yet another proposal has divided PPC into three dorsal streams that support spatial working memory, visually guided action and navigation, respectively (Kravitz et al., 2011). Finally, it has recently been suggested that there are not fixed streams in PPC, but that, instead, interconnected neuronal networks emerge to address multiple functional requirements (Galletti and Fattori, 2018). The same neurons may be part of multiple such instantiated networks and dynamically adapt their behavior and, thus, their functional role, according to the action class that is selected. This idea is graphically depicted in Fig. 1b, showing that units contribute to different action classes (as indicated by the traced regions). Accordingly, it seems probable that understanding mechanisms of ad-hoc connectivity, as well as the connectivity patterns associated with particular functions or action classes, will be necessary for a complete picture of PPC function (Engel et al., 2001; Heed et al., 2015; Wong et al., 2016).

Taking all these ideas one step further, if one considers an even wider set of effectors and functions than those in the studies reviewed here, they may as a whole be optimized according to a set of learned rules that capture statistical regularities in behavior, as seen in the gradual development of primary somatosensory cortex in postnatal developing rats (Seelke et al., 2012), and suggested by computational modelling (Lafraquière et al., 2018; Makin et al., 2013; Tenenbaum et al., 2011; Terekhov and O'Regan, 2016). In such a framework, gradients from one sensory system to another, or from world- to body-centered state estimation emerge from the statistical relationships between the respective driving forces.

2.3. PPC flexibly interfaces sensory information with action

So far, we have described PPC as a region that merges sensory and motor information. However, a defining aspect of PPC and of the circuits it builds with frontal cortex (Vijayakumar et al., 2019) is a role in action selection, presumably implemented as a continuous competition between goal or action alternatives (Cisek and Kalaska, 2010; Pezzulo and Cisek, 2016; Stepniewska et al., 2011). Decisions between available alternatives require that the brain evaluates and prioritizes potential actions towards them (Bisley and Mirpour, 2019; Sugrue et al., 2004) based on their expected value as well as their associated cost, such as energy consumption and danger to the body. This requirement links back to perceptual aspects of PPC function and the concept of saliency maps that spatially integrate multiple stimulus-related characteristics (Gottlieb, 2007). Thus, again PPC exhibits hybrid functionality that can be accentuated as pertaining to perception or action.

However, a critical ability of intelligent behavior is a high flexibility in linking between sensory information and action. The spatial coding of PPC is dynamic (Cappadocia et al., 2017), and adapts to the present task context (Bernier and Grafton, 2010; Leoné et al., 2015). For instance, a grasping-related region in the anterior IPS exhibited gaze-centered coding for visually, but body-centered coding for som aesthetically-defined grasp targets (Leoné et al., 2015). However, beyond the role of PPC in matching spatial information to body and world, several lines of work have demonstrated that PPC can abstract from spatial information, for instance by categorizing sensory input (Freedman and Assad, 2011; Freedman and Ibos, 2018), deriving spatial relationships (Chafee et al., 2007; Chafee and Crowe, 2013; Chivukula et al., 2019), and flexibly linking sensory cues to arbitrary responses (Haar and Donchin, 2019; Oristaglio et al., 2006; Stoet and Snyder, 2004). This ability to interface perception with action is usually referred to as (top-down) task-dependence, cognitive set, or even more broadly as cognition.

But how, then, can task-dependence fit into our proposed 2-dimensional organizational scheme? There is ongoing debate about whether decision-related signals in PPC reflect genuine decision formation, or information originating from other regions, for instance prefrontal cortex and the basal ganglia (Crowe et al., 2013; Erlich et al., 2015; Katz et al., 2016). A framework in which PPC primarily receives decision information fits well with a role in state estimation, that is, supporting the here-and-now for whichever goal has been defined. It is noteworthy that the more caudal area PRR has been reported to show activity related to several potential reach targets (Baldauf et al., 2008), whereas more rostral area 5d appears to code only the finally selected reach plan (Cui and Andersen, 2011). This increasing selectivity pertaining to the definition of an effector-action goal pair is consistent with the increasing effector-specificity from caudal to rostral, as discussed above (Heed et al., 2016b; Leoné et al., 2014a). In our view, then, task-dependence represents the conglomerate of sensorimotor functions we have discussed so far, completed by top-down control from other, presumably frontal regions. This implies that action selection and action specification proceed based on state estimation, which encompasses (multi-)sensory information about the body, about the environment, and top-down regulated behavioral requirements. As a consequence, task-specific activity should be subordinate to our proposed rostro-caudal and medio-lateral gradients. Accordingly, task-specific activity should be observable all across PPC, depending on whether, for instance, the present situation requires body-related or environment-directed function, and depending on which body parts the present task implies. In other words, we suggest that task-related activity does not reflect an explicit representation of task – in the sense of the researcher's semantic construct of what is observed – but rather emerges from the involved sensory, motor and cognitive aspects of the present state. This proposal links back to the previously discussed idea of ad-hoc instantiated processing streams or networks (Galletti and Fattori, 2018).

Indeed, quite regularly, effector choice and definition of present action alternatives depend largely, if not entirely, on the task. For instance, when we are carrying a heavy box with two hands, we will not attempt to catch a ball that is thrown towards us. You won't catch a ball with your foot and cannot swipe away an insect on the arm with that same arm. Task-context determines whether an available behavioral option is viewed as a viable alternative or not. These very simple examples show how intertwined sensory, motor, and cognitive aspects are, and demonstrate the feasibility of their common implementation in one common brain structure. State estimation subsumes all these aspects under a common roof, and may, thus, serve as an overarching theoretical construct along which PPC function can be described.

2.4. The organization of PPC in a larger scheme

In OFC, there is a computational difference between forward modeling, which has been suggested to be dominated by the cerebellum, action selection, perhaps a function predominately by the basal ganglia and frontal cortex, the control policy, thought to be mediated by primary motor cortex, brainstem, and local spinal circuits, and finally state estimation, suggested to reside mainly in the PPC (Haar and Donchin, 2019; Scott, 2012; Shadmehr and Krakauer, 2008). Note that a critical challenge for any implementation of state estimation is compensating for sensorimotor noise and temporal delays between commands and effects. Recent proposals suggest that adaptive filtering of sensory prediction in combination with a weight reduction of the sensory feedback can solve this issue (Crevecoeur and Kording, 2017; Crevecoeur and Gevers, 2019).

We have presently restricted our proposal to the dorsal surface of PPC. This region has received the ample attention in the distinction of dorsal and ventral processing streams for action vs. object recognition and is highly relevant for online control of hand and eye movement. However, it may be possible to extend our proposal also to the medial side of PPC, that is, the precuneus. At the whole-brain level, resting state studies have suggested that the human brain is intrinsically organized into dynamic, anticorrelated functional networks (Fox et al., 2005). Based on these studies, regions along the IPS exhibit task-related activations for externally oriented tasks, whereas inferior parietal cortex and precuneus show deactivations but instead activate for internally-oriented mental processes, such as future-oriented thoughts and actions (Xu et al., 2016). While state estimation involves processing of the present as well processing the future consequences of actions it fits this general account, although it remains to be examined how these resting state differences pan out at a finer scale.

Moreover, precuneus is active when human participants must orient themselves relative to objects in the environment during whole body motion (Wolbers et al., 2008), and it has been suggested that precuneus entertains a coarse map of objects in the environment (Land, 2014). This region, thus, may constitute another pole of state estimation, in which the body as a whole must be related to the larger environment (Burgess, 2006), including regions of unseen space (Schindler and Bartels, 2013). In contrast, dorsal-caudal PPC estimates the immediate environment on which actions are to be performed. Ultimately, then, the role of PPC is to relate the individual's own body to the world, with different larger areas being responsible for distinct clusters of actions: rostral-dorsal for "world on body", that is, body-related tasks; caudal-dorsal for "body in immediate environment", that is, body-object interaction; and medial for "body in space", that is, navigation. This potential, third pole may, in addition, prove relevant when locomotion is required to enable new affordances (Pezzulo and Cisek, 2016), such as approaching an object to grasp it. Neither brain activity nor single neuron activity have been assessed in such comparably complex environment-object-body interactions.

3. Concluding remarks and future directions

Posterior parietal function emerges from the interplay of sensory and motor functions. We propose that its main role is the estimation of the state of body and environment in the current task context. More specifically, rostral and caudal poles of PPC reflect opposite requirements of state estimation that relate to choosing actions by assessing current options in the environment, and to specifying actions by optimizing body-environment interactions. According to this view, the separation into perceptual and action-related functions and their relative dominance should step in the background in attempts to understand the PPC, as they are ultimately two sides of the same coin.

As one concrete example, PPC is known to play a role in the representation of the peripersonal space (Cléry et al., 2015; Graziano and Cooke, 2006). It has recently been pointed out that the definition of this concept is inconsistent across the literature (Bufacchi and Iannetti, 2018). A sensory aspect of peripersonal space is the existence of receptive fields that feature tactile RFs and, at the same time, visual RFs that extend more or less far around their tactile counterpart (Cléry et al., 2018; Duhamel et al., 1998; Graziano and Cooke, 2006). A motor aspect of peripersonal space is that electrical stimulation of the regions containing the bimodal RF evokes defensive movements (Cooke et al., 2003; Graziano et al., 2002). An integrative view in which separation of sensory and motor aspects no longer takes a prominent role is one in which both sensory and motor characteristics are viewed together to derive multiple functional roles they might support (Bufacchi and Iannetti, 2018).

Here, we argue that state estimation encompasses the sensory, functional and motor role of the PPC. One challenge to our proposal is to fit higher-level cognitive functions, that have also implicated the PPC, into this framework. For instance, PPC is known to contribute to language (Binder et al., 2009), mathematical cognition (Simon et al., 2002), and reasoning (Wendelken, 2015). These functions likely rely on inference computations based on verbal and non-verbal representations (Paulesu et al., 1993), which may emerge from multisensory and motor information encoded in the PPC. Some approaches exist that attempt to explain how higher cognitive functions may be grounded in basic bodily processing (Freedman and Ibo, 2018; Pulvermüller and Fadiga, 2010), but the field is a long way from matching low-level cognitive functions and their related PPC areas to emergent, higher cognitive function.

Our framework challenges previous concepts of distinctions that may be relevant to PPC, and re-focusing in this way provokes new questions. For instance, how do the specific sensory connections of a particular area enable different functions, on the one hand through task-specific weighting of the different inputs, and on the other hand through anatomical, but also – and possibly predominately – functional connectivity with output-related regions (Battaglia-Mayer and Caminiti, 2019)? How do the sensory connections of a particular area enable this area's particular state estimates? How flexible are the connections between the body-related and environment-related state estimates? If neurons in a given state code for multiple effectors, how is a choice between them mediated? Do dynamic changes in neural coding support integration of body and environment poles, and if so, how? Incidentally, our framework also challenges current models of motor control, which at present conceptualize state estimation as a singular functional unit (Shadmehr and Krakauer, 2008), and suggests that revisions of motor control models should account for at least two poles of body vs. immediate environment, and potentially for a third pole related to the body in the larger world. Such a revision could potentially merge other theoretical concepts about body representation, such as an action-related body schema, into motor control models (Martel et al., 2019, 2017) and our stable perception of the world (Land, 2014).

The overall explanandum is how PPC estimates the state of body and environment, contributes to choosing the next best action, and supports optimal control of its execution. Future work will have to

integrate behavioral function, competitive decision-making, and effector-specificity into a new concept of task-dependent action representation to address this goal.

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Appendix A. The Peer Review Overview

The Peer Review Overview associated with this article can be found in the online version <https://doi.org/10.1016/j.pneurobio.2019.101691>.

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