CHAPTER 18

THE BODILY SENSES

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There is no single sense for perceiving our own bodies, any more than there is a single sense for perceiving the external world. Nonetheless, folk wisdom groups bodily sensations together—unlike the five external senses, which are intuitively distinct. In part this may be because the systems that produce an experience of arm position, an itch, or an upset stomach, lack obvious sensory organs. In addition, bodily sensations are private (you can see what I see, but you cannot feel my body as I do), and the properties of our bodies that they track are often obscure. In this chapter we focus on three broad systems of bodily perception: interoception, the vestibular system, and proprioception. Our main goal is to argue that they constitute (collections of) sense modalities, while discussing some of the philosophical issues they raise.

1 The interoceptive senses

In order to function, the body must maintain physiological parameters within certain boundaries. Interoception is the collection of sensory systems that monitor the physiological state of the body in order to maintain this internal homeostasis. The term 'interoceptor' was first used by Sherrington (1906) to distinguish afferent pathways that carry information from the body to the brain, and was restricted to information produced by properties of the viscera: the respiratory, gastrointestinal, and cardiovascular organs. We take interoception to also embrace processes that originate in the skin, including those pathways that result in thermal sensations, cutaneous itch, and pain, rejecting the traditional view that pain and thermoception are aspects of touch. (For pain see chapter III.6; for touch, see chapter III.3, which defines touch as the perception of pressure, thus excluding pain and thermoception.) This might seem unintuitive, but excluding cutaneous systems of pain, itch and thermoception from the class of interoceptive systems would make a rather arbitrary cut, since these systems also monitor the viscera. Some go further (e.g. Cameron, 2001), and include proprioception and the vestibular system as part of interoception, but this taxonomy is too broad. What visceral and cutaneous monitoring systems have in common is that they constitute the afferent pathways used for regulating and maintaining the homeostasis of our internal organs and body parts (Craig, 2002). Prioprioception and the vestibular system, while 'body-directed', serve different functions, as we shall see.

Indeed, there is a seeming disconnect between the functional and extensional definitions of 'interoception'. In practice, researchers seem to restrict the extension of the term to internal monitoring systems of the viscera (e.g. Vaitl, 1996); but when it is defined functionally, the emphasis is on the internal monitoring and regulation of bodily organs for the purpose of maintaining homeostasis. Yet the skin, too, is an organ, one that shields internal structures, among many other functions. Thus we include detector systems in the skin as part of interoception, when functionally defined.

Interoception is most familiar to philosophers through the conscious bodily sensations it produces. Itches, thermal sensations, sensations of orgasm, heart-beat, thirst, indigestion, shortness of breath, and any form of pain, along with aspects of moods, emotions, and affect more generally, are all forms of interoceptive experience. The label 'bodily sensation' is unfortunate, however, since it invites the grouping together of many different phenomena (including the vestibular system and proprioception) under one label, as if they could be treated uniformly. Most discussion of interoception in philosophy has focused on the introspectable qualities of bodily experiences. However, as we will see, focusing on the extent to which interoception consists of a set of distinct sense modalities can throw new light on philosophical disagreements about the nature of bodily experience. Later we turn to the connections between interoception, emotion, and cognition.

Multiple modalities

Does interoception qualify as a sense modality at all? If so, should it be considered a collection of distinct sense modalities? The answers to these questions depend on how sense modalities are to be identified. One of us has defended a prototype account, which we adopt here (Picciuto and Carruthers, forthcoming). This account does not offer necessary and sufficient conditions for identifying sense modalities, but rather a list of characteristics that prototypical sense modalities possess. Candidate modalities are evaluated by the *degree* to which they have the following features:

1) Sensitivity to a set or range of related physical properties.
2) Detector mechanisms that transduce these physical properties into an informational signal to the central nervous system.
3) The evolved function of detecting and representing the physical properties specified by (1).
4) Representations with nonconceptual (or 'fine-grained') content and a mind-to-world direction of fit.
5) Utilization of the informational signals by the organism (typically through integration with other sensory inputs) to guide intentional action.

Modalities will be distinct to the extent that they differ from one another in these features (for example, by being sensitive to different ranges of properties, or by involving distinct kinds of transducer).

Many would also wish to insist that a sense modality should produce mental states with distinctive phenomenal qualities or 'feels'. But this criterion begs the question of the correct form of account of phenomenal consciousness. If first-order theories are on the right track (Tye, 1995), then phenomenal consciousness will be widespread in the animal kingdom. But if some form of higher-order account is correct (Carruthers, 2005), then phenomenal consciousness will be severely restricted in its distribution, perhaps to the primate clade. In the latter case it would not be appropriate to include possession of phenomenal qualities among the prototypical properties of a sensory modality. Since we do not wish to take a stand on this issue, we will include possession of phenomenal character in the discussions to come, while noting that its inclusion is controversial. (For a similar view, see chapter V.1.)

Is interoception a collection of systems sensitive to a range of physical properties of the body? Many have claimed that bodily sensations are unique in representing nothing beyond themselves. Thus Armstrong (1962) initially suggests that while thermal sensations track secondary qualities of temperature, the same does not seem true of other bodily sensations: an itch in my arm does not track an itchiness quality in my arm. Moreover, there does not seem to be an appearance–reality distinction for bodily sensations in the same way as there is for our external senses (a claim we return to): if something feels itchy, it *is* itchy. Similarly, one might claim, bodily sensations cannot go unfelt. True, one might be *distracted* from the itch on one's arm from a mosquito bite, but it is tempting to think that it does not make sense to talk of an unconscious itch.

We think that such intuitions are only plausible if one ignores the nature of the interoceptive systems that produces our bodily experiences. The fact that our folk psychological theory finds no object of bodily sensation does not entail that there are no physical properties to which interoception is sensitive. In fact, quite the opposite is true, once we consider the different kinds of receptor cell that provide input to interoception.

Since interoception tracks the functioning of many different internal organs, it relies on several kinds of receptor to transduce physical properties of the body into informational signals, which are sent to the brain through spinal pathways that are now well characterized (Craig, 2002). The classic work on species of interoceptors is Chernigovskiy (1967) who identified four main classes: mechanoreceptors, chemoreceptors, thermoreceptors, and osmoreceptors. What follows is a (non-exhaustive) list of different kinds of receptor cell, which also provides a picture of the different physical properties of the body that interoceptive systems track:

- Nociceptors are free nerve endings of small-diameter C-fibres and Aδ-fibres (most commonly associated with cutaneous pain sensation), which are found throughout the body's tissue (and viscerally). They respond to mechanical stress as well as local metabolic properties, cutaneous parasite penetration, and immune system and hormonal activity. Importantly, this includes a class of histamine-responsive C-fibres found in the human skin, which provide the inputs for our sensation of cutaneous itch.
- Thermoreceptors, found in the skin and viscerally, respond to temperature and temperature change of the body, with one set representing temperatures in the noxious range of cold or hot (thermal pain nociceptors), and another set representing changes within the innocuous range.

- Osmoreceptors track extracellular fluid osmotility relative to a homeostatic norm. Transduction is achieved via mechanoreceptors that respond to changes in cell volume. Osmoreceptors are found viscerally and in areas of the central nervous system that are outside the blood-brain barrier.
- Glucoreceptors are neurons that use glucose as a signalling molecule, based on its concentration density. Glucosensing neurons can be found viscerally in the intestine, gut, and liver, among other places, as well as in the central nervous system.
- Baroreceptors are nerve endings that respond to physical deformations and stress of the walls of the vessels in which they are located in order to track barometric pressure. These receptors are found throughout the blood vessels in the body.
- Tension mechanoreceptors, found throughout the viscera, respond to changes in muscle tension due to stretch, stimulation of mucosa, or both. They can be found in the bladder, stomach, and oesophagus.

Although the relationships between these transducers and our conscious interoceptive sensations are not transparent, it should nonetheless be clear that interoception tracks many different kinds of physical property, and that it involves a varied class of transducers that project to the central nervous system.

At this point, however, one might resist our claim that the properties detected by all these systems are internal. For much of what we seem to sense via thermoception are properties of external things, such as a cool breeze, or the handle of a hot kettle; it is the air that is cold, and the metal that is hot, rather than one's skin. Now, the same intuition does not seem to hold for itches, as we do localize histamine-responses to the skin. Nonetheless, it might seem we must exclude thermoception and perhaps other cutaneous senses from interoception, and include them as part of touch, for example.

In reply, we would again emphasize our earlier point that this categorization scheme requires us to classify some instances of thermoception are part of interoception and some not. We would also argue that the exteroceptive use of thermoception does not make it a non-bodily sense, or part of touch, any more than the fact that spatial orientation is facilitated by combining touch with proprioception makes touch part of proprioception (c.f. chapter III.3). Held in isolation, thermoception might give us little in the way of a sense of an external object independent of haptic feedback and proprioceptive awareness. We might have little sense of a *thermal object*. For example, imagine that a deafferented patient (one whose afferent pathways for proprioception have become de-mylinated; see below) is touched on her back (out of her vision field) with an cold iron rod (thermoception is typically not altered in deafferented patients). We can imagine: does the subject feel a cold object, or feel some body part as being cold? Absent a tactile sensation of the contact of the cold rod, or an ability to spatially localize the sensation (from proprioception), it seems the sensation would be felt as a state of her body. So it seems likely that thermoception only aids in exteroception when combined with other inputs. And, of course, thermoception is not restricted to the skin. It also underlies the feeling that we ourselves are too hot or cold. Hence thermoception should be classified as an interoceptive modality.

Given the existence of the above receptors and their accompanying pathways to the central nervous system, it should be clear that interoceptive systems evolved for the function of detecting many different physiological properties of internal and peripheral organs in order to maintain the internal homeostasis of the body, satisfying conditions (1)–(3) above.

But what about (4): do they also *represent* such properties? This depends on whether interoceptive states are representational at all, which some have disputed. For example, Akins (1996) argues that thermoception is non-representational because it fails to track temperature (of the body) in the veridical fashion that philosophers often have in mind when discussing representation. Thermoreceptors have a non-linear response profile to temperature and temperature change, and an uneven distribution over the body, with greater concentration at the head, groin, and armpits. (This is part of the reason why when one enters a lake, the water feels colder at these areas.) In this respect, thermoception, like all forms of interoception, is 'narcissitic', tracking physical properties motivated by the needs of the organism (or its organs) rather than objectively reflecting those properties. Thus, if thermoception fails to represent, so do interoceptive systems generally.

We think that the requirement of veridicality for representation is dubious, however. Unlike external modalities, the interoceptive senses are primarily sensitive to *disturbances,* becoming active when things in the body go wrong. When we eat some bad fish, catch the 'flu, or overly exert ourselves, the body is awash with interoceptive sensations. Under normal conditions we are barely aware of any feelings in the viscera, because most visceral afferents are typically 'silent', and respond only under very specific conditions. Thus afferents in the colon are active during bladder inflammation, but cease activity after the inflammation has ended. Likewise, interoception has not evolved to detect osmotic pressure as such, but to detect changes in osmotility that are significant deviations from the homeostatic norm. Thus lower osmotic pressure signals dehydration, causing thirst. Such event-like properties involving deviation from a norm are perfectly legitimate contents of mental representations, we believe.

Another challenge to the representational status of interoceptive experiences is that it does not seem possible to *misfeel* some bodily experiences, like itches (Armstrong, 1962). Block (2006), too, argues that this apparent fact is a problem for representationalists about consciousness, who hold that the phenomenal character of consciousness is exhausted by its representational content. Armstrong (1962) eventually argues that there is enough of an appearance-gap between bodily sensations and physical stimuli to enable them to misrepresent. What Armstrong advocates is that we 'translate' between a bodily sensation and the physiological state of the body that causes the sensation. For example, one might feel nauseous, and it would seem that if one feels nauseous one *is* nauseous. However, nausea represents that one's stomach is unsettled, and it is possible that one feels nauseous even when one's stomach is not unsettled. Such a proposal is even more plausible when we keep in mind that there is a whole collection of systems that detect physical properties of the body and produce such sensations.

Moreover, there are a number of features of interoception that serve to decrease the actual incidence of misfeeling. First, most forms of interoception detect stimuli that are proximate to the relevant transducers, since the latter are characteristically embedded within the organs that they monitor. This suggests that there is no proximal–distal distinction in such cases (in contrast with vision and hearing). Second, most forms of interoceptive awareness are comparatively coarse grained. Yet, that we rarely 'misfeel' does not imply that it is impossible, as Armstrong notes. While cases of robust interoceptive illusions are rare, there are cases of 'phantom organs' after surgery (Dorpat, 1971), and stroking exposed intestine can cause the illusion that defecation is needed (Airapetyantz and Bykov, 1945). Moreover, phantom limb patients often report sensations of phantom pain or itch. In addition, research on the psychophysics of interoception, which has primarily been on heart-rate monitoring, supports the existence of a great deal of between-subject variability. (Similar results obtain for respiratory and gastrointestinal monitoring; see Vaitl, 1996.) For example, gender, weight, age, and fitness affect cardiac interoception (Cameron, 2002).

Of course our bodily experiences often lack the sort of 'transparency' that is distinctive of visual experience. When one visually perceives something, one generally does not focus on the qualities of the experience itself, but rather on its objects, such as shape and colour. This transparency has been important to the case for representationalist theories of consciousness (Tye, 2002). When we focus on an itch, in contrast, we seem to be focusing on our experience itself. But this may result more from our folk-ignorance of the physical properties detected than the non-representational character of bodily experience. For notice that where folk-wisdom *does* provide an intuitive object—such as the gurgling in one's stomach or the thumping of one's heart after exercise—transparency seems to be present. When one focuses attention on one's beating heart it is the beats of one's heart that one focuses on, not one's experience as such.

The case for the non-representational character of bodily experience is not compelling, then. Furthermore, an important consideration *supporting* representationalism is the apparent localization of bodily sensations within the body. For example, feelings of constipation are localized to the colon, and such sensations are, of course, nonconceptual in character—or at least 'fine-grained' in comparison with the concepts that figure in our beliefs. Yet it seems implausible that our sensations should *literally* be located in a specific body part, as opposed to being *represented* as occurring there. This consideration is reinforced by the phenomenon of phantom-limb pain or phantom-limb itch, where the sensations are experienced as occurring in a limb that is no longer present.

We suggest, then, that interoception has most of the qualities of a prototypical sense modality (or rather, of a set of such modalities). But what about guiding intentional action? Initially it might seem that interoception fails condition (5). For the primary function of most interoceptive modalities is to provide input for the automatic and unconscious homeostatic regulation of the physiological condition of the body—not for guiding action. Admittedly, interoception effects action indirectly, as when we stop running to catch our breath, or eat because we are hungry. But this does not so much guide, as give us cause for, intentional action.

At this point it will be useful to recall the distinction drawn earlier between visceral and cutaneous interoceptive systems. For the latter forms of bodily experience can certainly guide action, and this is probably part of their function. Conscious experiences of pain and of heat are often used to guide actions, such as removing oneself (or a specific body part) from a source of pain, or removing a layer of clothing when hot. So cutaneous interoception certainly seems to consist of a set of prototypical sense modalities. It might be thought that matters are otherwise, however, with some forms of visceroception, whose outputs may never be centrally accessible and do not seem to guide intentional actions targeted on the world. Nevertheless, we do use visceroception to guide intentional actions directed at our own *bodies*. For localizing these sensations at different positions inside the body allows us to take actions (where possible) directed toward these areas.

We suggest, then, that all forms of interoception should qualify as sense modalities to some important degree, and that most should be fully categorized as such. There seems to be a spectrum (both *within* and *between* interoceptive modalities), from bodily sensations offering a distinct phenomenology that can influence controlled action (e.g. those underlying cutaneous itch), to those states that *can* be made conscious (cardiac perception), and then those that are produced by low-level detector systems and never rise to the level of awareness (monitoring osmotic pressure). Interestingly, while it can be doubted whether some of these interoceptive systems play much of a role in guiding intentional action, many of the same systems have been co-opted by other processes that do clearly play a role in action planning, as we will see in the following section. This reflects the central role of interoception in the embodiment of the mind.

Interoception, emotion, and cognition

The common-sense view of emotions is that they are feelings. James (1884) and Lange (1885) independently tried to develop this view, claiming that emotions are constituted by our awareness of interoceptive feelings, with different combinations of autonomic responses being distinctive of different emotions. For example, evaluating something in one's environment as a threat causes a distinctive set of physiological changes, which interoception tracks, and it is one's conscious interoceptive experience that constitutes one's fear. As James famously argued, if you subtract away these interoceptive experiences, nothing is left of one's fear. While the James–Lange theory has fallen out of favour, the current consensus in emotion theory is that our experience of emotion is constituted both by an affective component (partially reflecting interoceptive experience) and by a set of appraisal dimensions through which one conceptualizes and categorizes one's affective experience, which form a cognitive component of emotion (Izard, 2007).

Despite the widespread agreement in emotion theory that interoceptive sensations are partially constitutive of emotional states, the thesis that we can *individuate* emotions based on their felt bodily changes or a corresponding autonomic nervous system response (as the James–Lange theory claims), has remained controversial. Again, such a view seems to accord with common sense: being in a state of anger does not seem to *feel* the same as being in a state of joy. However, whether there are distinctive interoceptive sensations for distinct emotions partially depends on how one thinks about the ontology of emotions. Many theorists make a distinction between *basic* emotions such as fear, anger, sadness, disgust, surprise, and joy, and more complex, culturally dependent, emotions such as envy, guilt, and shame. But some argue that only the more evolutionarily ancient basic emotions have distinct autonomic responses and perhaps interoceptive experiences (c.f. Griffths, 1997); or going further, some argue that even the basic emotions lack distinctive interoceptive qualities (Barrett, 2006).

What is plausible is that a general sense of arousal, requiring contextual interpretation, is the primary contribution of interoception to emotion (Schachter and Singer, 1962). Moreover, Barrett (1998) has argued that individuals vary significantly in the extent to which they are sensitive to the arousal properties of their emotional states. A related finding is that the extent to which individuals rely on general arousal in categorizing their emotional experiences correlates with their interoceptive sensitivity on a cardiac monitoring task (Barrett et al., 2004). In sum, evidence supporting the James–Lange view that distinct emotions are characterized by distinctive interoceptive sensations has proven hard to come by (Larsen et al., 2008; Barrett, 2006).

A more recent suggestion is that interoception is the basis for one dimension of 'core affect' (Barrett and Russell, 1999). All forms of affective experience seem to vary along dimensions of *valence* and *arousal*. Valence can be either positive or negative, is tied to the reward system in the brain, and seems to be the main determinant of the choices that we make. Moreover, it is often identified with pleasure and displeasure. Whether it is a product of interoception, however, is doubtful; and one of us has argued that it should more properly be seen as a nonconceptual representation of *value,* rather than construed in hedonic terms (Carruthers, 2011). In contrast, feelings distinctive of arousal are certainly produced by interoception, though this arousal component of core affect comprises a heterogeneous collection of interoceptive sensations, rather than reflecting a single dimension of experience.

It is plausible, then, that interoception underlies one dimension of core affect. At the same time, core affect is thought to play a role in cognition more generally. On the one hand, affective experiences seem to provide a constant background context to thought and action. On the other hand, it is also said to play a role in *how* we reason and make decisions, allowing us to evaluate the desirability of different choices or judgements. For example, according to the influential 'somatic marker' model proposed by Damasio (1994), we choose among options by imagining them, responding affectively to these imagined scenarios, and by monitoring our affective responses. In evaluating this proposal, however, much depends on the nature of the affective response. Much of the evidence of the role of affect in cognition suggests that our decisions are guided primarily by the valence dimension. But arousal, too, plays an important role. According to the affect-as-information approach, arousal carries information about *urgency* (Storbeck and Clore, 2008). Intuitively, this makes sense: I may for example desire to view a crucial scene in a movie more than I do going to the bathroom, but under appropriate circumstances, satisfying the latter desire becomes far more pressing. Seemingly in support of this picture, Werner et al. (2009) found that subjects with better cardiac perception performed better in the Iowa Gambling Task, the same task that has been used to provide evidence for the somatic marker hypothesis.

Moreover, arousal plays an important role in judgements *about* how we feel about something, rather than influencing our first-order judgements themselves. In this regard, arousal might make conscious our implicit reaction to a stimulus (Storbeck and Clore, 2008). This coheres well with the role that interoceptive outputs (including changes in arousal) have been thought to play in metacognition, or 'thinking about thinking' (Koriat, 2007). When we metacognize, we form representations of our own mental states in the service of controlling our own learning, remembering, or reasoning. The most familiar examples are long-term memory phenomena like the feeling of knowing (e.g. for a name you know, but cannot remember). Changes in affect can be caused by changes in how fluently we process information, and such affective changes are used as cues for inferring how successfully we are learning or thinking. In these cases interoceptive processes have been co-opted and are utilized to evaluate our own cognition, rather than the physiological state of the body.

Conclusion

We have argued that interoception should be seen as a set of distinct sense modalities for monitoring and maintaining the homeostasis of bodily organs. However, the role of interoception in emotion-individuation, as well as in reasoning and decision making, may be more limited than some have claimed.

2 The vestibular sense

The vestibular system is perhaps one of the most interesting of the human sensory repertoire, and yet philosophers have paid it scant attention. It is crucial for our sense of balance, and receives its inputs from an elegant set of organs in the inner ear that respond to displacement of the head. This system is heavily integrated with ocular motor processes, as well as with vision and proprioception, and it is through this integration that the vestibular system contributes to spatial perception and navigation. Our discussion focuses on the prototypicality of the vestibular system as a sense modality.

A vestibular sense?

The vestibular system is sensitive to acceleration and rotation of the head, as well as perturbations caused by contact with the ground. In fact it is plain that the vestibular system meets the first three conditions of being a prototypical sense, in that it detects a form of physical stimulus (inertial motion of the head) through a set of distinctive transducers, and has seemingly evolved for the purpose. Much is now known about the early processing of the vestibular system, and how and why it integrates with other modalities in non-cortical brain areas (Angelaki and Cullen, 2008).

The primary peripheral component of the vestibular system is the 'labyrinth', a complex collection of chambers of the inner ear. This includes the two otolith organs, the utricle and saccule, which respond (respectively) to horizontal and vertical linear head displacement (due to tilting or translation), and the three semicircular canals, which each respond to head rotation along roughly orthogonal spatial axes (i.e. for roll, pitch, and yaw). This set of chambers is continuous with the cochlea, which is peripheral for audition. Like audition, vestibular transduction is via hair cells, a kind of mechanoreceptor. Thus the vestibular system clearly has a set of detector mechanisms that track the above mentioned physical properties.

Does the vestibular system produce representations with nonconceptual content and a mind-to-world direction of fit? It certainly seems to. Indeed, the vestibular system would appear to provide both mind-to-world *and* mind-to-body direction of fit. For it provides information about the direction of gravity in addition to the movement of the body (even in the absence of input from external modalities). Moreover, the representations in question are plainly of a fine-grained or nonconceptual sort, and are provided as input for conceptual judgements about body movement and orientation.

Finally, that vestibular outputs are used in guiding intentional action seems clear, given their role in spatial navigation. Consider, for example, how difficult it is to navigate when experiencing vertigo or dizziness, both of which (especially in some chronic conditions) can be produced by vestibular disruption. Experimentally, the role of vestibular outputs has been shown using experiments that require subjects to orient spatially in the absence of vision. For example, in a common paradigm, subjects successfully reorient to an initial starting position after being passively rotated in the absence of visual input (e.g. the room is dark, or subjects are blindfolded). And as might be expected, individuals with peripheral vestibular pathologies are impaired relative to normal subjects when it comes to walking a linear path with their eyes closed, but not with eyes open (Cohen, 2000).

We conclude that the vestibular system has all or most of the properties of a prototypical sense modality. Questions remain, however, about the nature of vestibular phenomenology. For some have claimed that by the time vestibular representations become conscious they have been tightly integrated with the outputs of the visual system and/or the proprioceptive system, in such a way that the resulting experiences are entirely visual or proprioceptive in nature.

A vestibular phenomenology?

Angelaki and Cullen (2008) claim that there is no such thing as vestibular phenomenology. This is because of early integration of vestibular outputs with other modalities. While our sense of orientation and balance is largely determined by vestibular processing, it is only manifest in our awareness through visual and proprioceptive phenomenology. Put differently: if one were to subtract the visual and proprioceptive contents from our experience, then nothing distinctively vestibular would remain. If this claim were true, then the vestibular system might provide an example of a sense that does not contribute to conscious awareness through modality-specific phenomenology. Indeed, if the claim were true, then the status of the vestibular system as a prototypical sense modality could be challenged. For it would mean that vestibular outputs, as such, do not guide action. Rather, they provide input to vision and proprioception, and it is the latter that guide action. So the guidance function of the vestibular system would only be indirect.

The claim of early integration seems insufficient to establish such a conclusion, however. For senses can be integrated and yet make distinctive contributions to our experience. (Think of taste and smell, for instance, or our earlier discussion of thermoception.) But another way of approaching the question is to consider what form of spatial reference frame vestibular processing utilizes. If it shares a reference frame with vision or proprioception, then that weakens the case for a distinctive contribution to phenomenology; whereas if it maintains its own reference frame then this would provide some support for the separateness of the contents produced.

Early in processing the vestibular system operates with a head-centred reference frame, but since the vestibular system is also utilized for navigation, and hence action, vestibular representations must at least interact with body-centred (or somatotopic) and eye-centred (or retinotopic) reference frames. A traditional view is that multi-modal integration depends on translation into a shared, ostensibly more abstract, reference frame, but Angelaki and Cullen (2008) themselves claim that evidence concerning vestibular integration with other modalities undermines this view. Inputs from the labyrinth and from neck proprioception allow the brain to relate the head-centred reference frame of the vestibular system to a somatotopic reference frame, which contains a neck component. This integration is provided by a mixture of modality specific and 'intermediate' reference frames. Another challenge to the idea of a common reference frame concerns visual–vestibular integration. Fetsch et al. (2007) found that vestibular signals have a head-centred topography, but at the population level have a more retinotopic structure. Their data suggest that different reference frames remain distinct during integration.

It remains possible, then, that the vestibular system makes a distinctive contribution to phenomenology. But this is hard to establish introspectively. In conditions like out-of-body experience, for example, in which subjects feel as though they are experiencing the world and their body from a separate position, as well as in autoscopy, in which subjects still experience themselves as 'at' their body, but feel that their body is in extrapersonal space (it is not 'part' of them), subjects primarily report visual phenomenology. However, subjects may also report sensations of floating, lightness, or flying (Blanke et al., 2004). Such reports seem intuitive and plausible, and many of us will be familiar with similar experiences when dreaming (such as the sensation of falling). However, here we might again apply James' thought experiment from earlier: when my head is actively or passively displaced, and I subtract the proprioceptive sensations of my neck, and of my feet on the ground, as well as any visual feedback, does a head-centred sense of *inertia* remain? This is by no means easy to answer.

To assess whether there is such a phenomenology, one could perhaps put subjects in a sensory deprivation chamber to see what kinds of self-report are generated. Given the head-centred reference frame of vestibular outputs, perhaps one would predict a sense of the direction of gravity, and whether displacement is due to tilt or translation. Alternatively, one might probe the phenomenology of pilots, who rely heavily on the vestibular system during flight. However, while such phenomenology can be described, it is hard to imagine what it would feel like beyond a mere abstract description of this sort. The general question raised here is what it *means* for a sense modality to have a distinct phenomenology, and how one would go about searching for it, either introspectively or experimentally.

Conclusion

While there are powerful reasons for recognizing the vestibular system as a distinct sense modality, it remains unclear whether it makes a direct and distinctive contribution to the phenomenology of our experience. (Indeed, this might partially explain why philosophers of perception have typically paid it so little attention.)

3 The proprioceptive senses

The body-directed sense that has been of most interest to philosophers is proprioception, the sense of the body's spatio-structural extension, which provides afferent feedback during movement for guiding action. Proprioception has not only been of interest to philosophers in the analytic tradition, but also the phenomenological tradition—particularly in the work of Husserl (1989) and Merleau-Ponty (1962). (For phenomenological approaches to perception, see chapter I.7.)

Philosophers have offered markedly different views about the nature and possibility of a proprioceptive sense. Some claim that we do not have a sense modality for bodily position, because this implies the possibility of misrepresenting it (Anscombe, 1962). Others think that we have a special nonperceptual form of sensorimotor access to our own bodies (Merleau-Ponty, 1962). Thus there is no *perceptual* experience of one's legs being crossed, only an awareness of the fact that one's legs are crossed. We think, in contrast, that it is quite clear that proprioception is a prototypical sense modality.

A proprioceptive sense

Proprioception is sensitive to (a range of) physical properties of the body, and receives input from detector mechanisms that transduce these properties into informational signals. Proprioceptive inputs come from the primary and secondary afferents of muscle spindles, cutaneous receptors that track skin elasticity, as well as mechanoreceptors in the joints. While it was previously believed that joint receptors play a major role in tracking position and movement, it is now known that muscle spindles are in fact the dominant input for proprioception (Proske and Gandevia, 2009). For example, vibrating the muscle spindles of blindfolded subjects produces illusions of arm movement and position. If this is paired with tactile contact between the vibrated limb and some other body part, stimulation induces illusions of body deformation. One example of this is the Pinocchio illusion, in which one experiences one's nose growing outward while remaining in contact with the felt movement of one's hand (Lackner, 1988).

While information from muscle spindles provides the dominant afferent inputs for proprioception, when muscles span across multiple joints, muscle spindles can provide ambiguous inputs regarding joint contraction. In the case of fingers, the muscles are located in the hand and forearm, and the tendons extend across multiple finger joints. Thus for finger proprioception, cutaneous receptors that track skin elasticity seem to provide crucial information regarding finger position and movement, which cannot be extracted from the muscle spindles in the hand or forearm alone. Joint receptors, in contrast, are thought to be primarily limit detectors. That is, if one tries to straighten one's arm beyond the limit of the joint, it is the sensation from the joint that informs us that the limit has been reached, not the experience of muscle stretch.

It would seem that proprioception, or its constitutive input systems, satisfies conditions (1)–(3). But what about conditions (4) and (5)? It is clear that the constitutive systems of proprioception produce fine-grained or nonconceptual representational content with mind-to-world (or rather mind-to-body) direction of fit. Moreover, by providing afferent feedback about body position, some role for proprioception in guiding action seems clear. Matters appear somewhat more complicated, however, when we ask whether proprioception should properly be counted as a single sense, or multiple senses. On the one hand, the three main types of proprioceptive transducer track distinct physical properties. And it is possible for us to be aware of their outputs individually (e.g. the tensing of individual muscle groups when we exercise). So in some respects proprioception can be considered as three distinct sense modalities. (Contrast here the clear unity of the vestibular system.) On the other hand, it seems that part of the *function* of proprioception is to produce an overall representation of the position of the body for planning and guiding action, integrating together the outputs of the various contributing transducer mechanisms. (In this respect proprioception seems to differ from interoceptive systems, which are not obviously integrated into a single overall representation of body homeostasis.)

Indeed, typically we are not aware of the components of proprioception. Rather, we are aware of the form and posture of our bodies. Furthermore, other sense modalities, such as touch, and aspects of interoception, require such form and posture representations to which they can be mapped. Deficits of different kinds put this fact in stark relief. Consider phantom limb patients, who still feel as though the amputated limb is present, or deafferented patients whose proprioceptive afferents have become de-mylinated, and so receive no proprioceptive (or tactile) inputs. In the former case, subjects report vividly the experience of a limb that they can see is not there, while in the latter, subjects have no awareness in the absence of vision of the bodies that they know themselves to possess. In such cases, subjects are clearly reporting deficits in body perception, which moves beyond sensations of stretched muscles or taught joints.

This question of integrated representations for form and posture is related to how proprioception satisfies conditions (4) and (5). It seems plain that proprioception is used for guiding intentional action; indeed, this seems to be its primary function. It enables us to keep track of the spatial relationships between body parts and (along with other modalities) *where* the body is in relation to other objects in the environment. However, when one reaches for a cup of tea, one is not typically aware of how much one is stretching one's muscles and aligning one's joints. Rather it is the overall position of one's arm and the form of one's grip that one is aware of. In philosophy and cognitive science, holistic perception and representation of our own bodies has been associated with the notion of the body schema. Thus we now turn to the question of the relationship between proprioception and this construct. (For more on perceiving the body as an object, see chapter IV.8.)

Proprioception and the body schema

Cognitive scientists have been increasingly interested in a distinction between the body *schema* and the body *image,* and it is in connection with these constructs that proprioceptive outputs have been thought to play an important role in conscious forms of perception and cognition, as well as in action. The origin of the distinction is in classical neurology (Head and Holmes, 1911–12), where it was thought to provide a way of explaining apparently contrasting deficits that somehow relate to the body. Unfortunately, use of the terminology has been confusing, with both terms having been used interchangeably or inconsistently by psychologists. (See Gallagher, 2005, for a useful review.) At first pass, the body schema is thought to be a long-term, regularly updated, unconscious representation of the body's extension and posture, which is used to guide action. It is often claimed to be multi-modal, relying on proprioceptive, visual, haptic, vestibular, and motoric outputs. By contrast, the body image is a set of largely conscious states and processes, including our intermittent awareness of the body, our concepts and beliefs about the body, and our emotional responses to the body, and is sometimes claimed to be largely visual in nature.

While evidence for this distinction has traditionally come from neuropsychology, in recent years a great deal of research has been carried out with normal subjects. We cannot do justice here to the explosion of experimental and theoretical work in cognitive science on the body schema (and image). We will focus more on conceptual issues, while touching on recent empirical findings.

We believe the distinction between body schema and body image as typically drawn is explanatorily inadequate. Clearly much of our conscious experience of our bodies is perceptual, while emotional or cognitive attitudes toward our own bodies are not. The heterogeneity of the body image suggests that it fails to constitute a natural kind. Moreover, it is much less closely related to proprioception. We therefore focus on the nature of the body schema and how it relates to proprioception as a sense modality. It should be noted, however, that there might be multiple body schemata, separately representing form and posture (Medina and Coslett, 2010).

A first question is whether the body schema is genuinely multi-modal or primarily proprioceptive in nature. Is its frame of reference constitutively determined by proprioception along with vision and touch, or do the latter modalities simply provide inputs to what is in fact a proprioceptive representation? Note that if deafferented patients are thought to have a deficit in their body schema (Gallagher, 2005), this would seem to support the body schema being a proprioceptive representation; indeed, the point that subjects must *compensate* for the deficit using vision suggests that vision is insufficient by itself. If vision were constitutive of the body schema, then one might think it would still be providing some inputs. But if the body schema is a proprioceptive representation, then it makes sense that this deficit should be so utterly crippling for one's awareness of one's own body.

In stark contrast, blind people are decidedly not blind to their own bodies, though they have a deficit in localizing them relative to objects in the environment. Furthermore, behavioural evidence suggests proprioceptive dominance. For example, during a motor imagery task proprioception, but not vision, influenced the coding of hand position during the task (Shenton et al., 2004). Also, in some situations where vision and proprioception provide conflicting information about body position (Hogendoorn et al., 2010), or size (Linkenauger et al., 2010), proprioception overrides vision. However, one might point out that there is also evidence that use of vision and proprioception to guide action is weighted based on which provides more reliable information about body position (van Beers et al., 1999).

Does the body schema enter into consciousness? Traditionally many have defined the body schema as unconscious, hence distinguishing it from the body image. But given that we have set the body image aside we can ask whether there is a principled distinction to be drawn between the unconscious body schema and proprioceptive experience. Longo and Haggard (2010) found that when subjects are asked to point to positions on their occluded hand below a table, the body map of the hand is distorted with shortened fingers, which seems to reflect an unconscious representation with a similar distortion of form, namely the homunculus of somatosensory cortex. This result might be interpreted in terms of an unconscious representation determining our conscious experience. It suggests at least that form and posture representations are 'built up' out of proprioceptive components, creating distortions of form when not integrated with vision.

Some have suggested that the body schema is part of the 'how'-pathway for somatosensory processing, by analogy to the dual-pathways model of vision (Dijkerman and de Haan, 2007). As Milner and Goodale (1995) have shown, we can distinguish between the visual processes that contribute to action and those that contribute to object identification. Interpreted in this way, the body schema would be part of the action or 'how'-pathway, and be unconscious, while proprioceptive experience would be part of the perception or 'what'-pathway, and be utilized in body recognition and localization. A complimentary addition to the dual-pathway view is that the body schema provides the afferent feedback for the forward model for motor control. The motor system generates two outputs. One, the 'inverse model', is a set of commands for motion given a prior representation of the body's position. The other, the 'forward model', is a representation of the predicted position of the body after completion of the movement (Wolpert et al., 1995). This forward model is compared with the actual position of the body as the movement unfolds, based on afferent inputs from proprioception (and also vision), and enabling swift online corrections and adjustments. De Vignemont (2010) plausibly suggests that the body schema provides inputs for both the initial planning of action and its correction as action proceeds.

Some evidence for this view, which ties the apparent unconscious nature of the body schema to its function of guiding action, comes from work on the rubber-hand illusion by Kammers et al. (2009). In their study the illusion was induced by synchronized stroking of a visible fake hand and the subject's occluded hand; this stimulation has been shown to induce a sense of ownership over the visible fake hand (Botvinick and Cohen, 1998). Next, the fake hand was also occluded and subjects were asked to indicate the location of the stimulated limb in one of two ways: either by verbally reporting whether or not the experimenter was pointing to their limb location, or by reaching with their un-stimulated limb. If the body schema is influenced by the illusion, then it should influence subjects' ballistic arm movements to bias them toward the fake hand, while if the illusion just influences their proprioceptive experience it would only have an effect on their verbal judgements. The finding was that ballistic arm-movements were not influenced by the illusion, which can be interpreted as supporting a dissociation between the body schema and proprioceptive experience. Despite this evidence, it is also likely that, as in the case of vision, these two pathways are not entirely encapsulated from one another (de Vignemont, 2010).

Conclusion

Proprioception is a prototypical sense modality whose primary function is to inform motor planning and guide action. The primary output of proprioception can be identified with the body schema, under some characterizations of the construct, but it also issues in conscious experience of body position. While we have focused on the status of proprioception as a sense modality, there has been much interesting work on bodily self-awareness as a kind of non-conceptual primitive self-consciousness, and on how proprioception relates to our sense of ownership and agency over bodies and actions, both in philosophy (Bermudez et al., 1995) and cognitive science (Tsakiris and Haggard, 2005). A related topic is whether our knowledge of the body afforded by our bodily senses is immune to error through mis-identification (Evans, 1982; Legrand, 2006). In short, proprioception, and indeed the bodily senses in general, seem to be of central importance not just for our perception of our bodies, but of ourselves. (See de Vignemont, 2011; and chapter IV.8.)

4 Conclusion

In this chapter we have discussed interoception, vestibular perception, and proprioception, arguing that each has a strong claim to be considered as (collections of) sense modalities, while also touching on a number of philosophical issues relating to these systems. In many cases these questions have not been widely discussed, since philosophers interested in perception have traditionally been focused on how we look out at the world. We believe that much interesting work remains to be done on how we look within.

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