What can vigilance tell us about fear?

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Abstract: Animal vigilance is concerned with the monitoring of potential threats caused by predators and conspecifics. Researchers have argued that threats are part of a landscape of fear tracking the level of risk posed by predators and conspecifics. Vigilance, which is expected to vary with the level of risk, could thus be used as a measure of fear. Here, I explore the relationship between vigilance and fear caused by predators and conspecifics. The joint occurrence of vigilance and other physiological responses to fear, such as increased heart rate and stress hormone release, would bolster the idea that vigilance can be a useful marker of fear. While there is some support for a positive relationship between vigilance and physiological correlates of fear, a common theme in much of the empirical research is that vigilance and physiological correlates of fear are often uncoupled. Uncoupling can arise for several reasons. In particular, vigilance is not always a sensitive or specific marker of the internal state of vigilance. Vigilance might occur in animals who do not appear overtly vigilant or conversely an animal might appear vigilant without necessarily maintaining a state of vigilance. Animals in a fearful state might also be unable to allocate time to vigilance if they are too hungry. Vigilant animals might not show physiological responses associated with fear if they become desensitized to threats. For all these reasons, inferring fear from vigilance is fraught with ambiguity.

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1. Introduction

The semipalmated sandpiper (*Calidris pusilla*) is a small North American shorebird who breeds in the Canadian arctic and winters along coastal South America (Hicklin & Gratto-Trevor, 2010). The Bay of Fundy, in eastern Canada, serves as a major stopover area during fall migration. Large sandpiper flocks forage on the Bay’s mudflats for small invertebrates and other minute food items (Gerwing, Kim, Hamilton, Barbeau, & Addison, 2016). When the tide covers the mudflats, sandpipers gather on the shore to rest in flocks that can exceed 250,000 birds (Sprague, Hamilton, & Diamond, 2008) (Figure 1). Rising tides force sandpipers to forage and rest close to the shore where they are vulnerable to surprise attacks by peregrine falcons (*Falco peregrinus*) and other raptors (D. Dekker, I. Dekker, Christie, & Ydenberg, 2011). Falcons launch surprise attacks from the wooded cover near shore; they fly low over the mudflats using vegetation cover to mask their rapid approaches (Beauchamp, 2016c). Small sandpipers cannot confront the much larger falcons. Instead, they rely on vigilance to detect attacks before it is too late to escape. Thousands of eyes in a flock thus scan the sky for signs of approaching falcons. Upon detection of a threat, the sandpipers cluster into a tight, swerving ball that protects the birds by making it more difficult for the falcons to isolate one prey (Leger & Nelson, 1982).

![Figure 1. Large flock of semipalmated sandpipers roosting on the shore.](image)

Falcons affect sandpipers in direct and indirect ways. The lethal effect of predation is obviously one direct consequence for the unlucky ones. However, sandpipers also adjust their behaviour to reduce the chances of capture, thus opening the door for indirect effects of predation (Lima, 1998). For instance, sandpipers interrupt their activities to scan the surroundings for signs of danger. Such vigilance comes at a cost, as it curtails essential
behaviour such as foraging and resting. While joining other foraging sandpipers allows individuals to reduce the chances that falcons approach undetected, it also increases competition between individuals (Beauchamp, 2007, 2012). These various indirect costs of predation might translate into a slower rate of fat deposition during stopover, perhaps increasing the length of the migration, and eventually reducing the odds of survival (Ydenberg, Butler, Lank, Smith, & Ireland, 2004).

Foraging in large flocks, sandpipers also face another type of threat, namely, one another. Aggressive displacement from a resource patch is common in these birds (Beauchamp, 2014b). One sandpiper will make a run at a nearby companion, often coming from behind to reduce the chances of being detected, and bump into the other bird to usurp the food patch. Aggressive displacement is less likely with longer runs, suggesting that investment in vigilance might be useful to detect these attacks early (Beauchamp, 2016a).

Are sandpipers anxious about predation threats or aggressive displacements? Are they fearful? Are they conscious of fear? While these answers would be obvious to us if we faced the prospect of ambush attacks by lions at a watering hole in the African savannah, it is not so clear when we try to address these issues in a different species. Non-human animals cannot provide reports about their feelings. Because invasive procedures to determine the recruitment of brain circuits are not always an option or even possible in the field, how is it possible to infer fear in animals? Behavioural patterns and other physiological adjustments triggered by the activation of brain circuits involved in the fear state could provide an indirect way of assessing fear. In sandpipers, for instance, looking for threats often leads to higher vigilance, which is betrayed by head cocks. Vigilance in general is relatively easy to document in the field. My aim here is to examine what vigilance can tell us about fear, not so much about the feeling of fear but rather about fear as an emotional state (Anderson & Adolphs, 2014; Gross & Canteras, 2012), which includes measurable physiological and behavioural correlates. In the first part, I provide a brief introduction to the topic of vigilance in animals. I then examine the evidence for a state of fear in animals and its relationship with threats from predators and competitors.

2. What is vigilance?

As defined in a dictionary, vigilance relates to the state or the action of keeping careful watch for potential danger. This is certainly the meaning that we attach to this word in a saying like “vigilance is of the essence.” In the scientific literature concerned with humans, vigilance often relates to the ability to detect stimuli of interest in the environment, which might only bear a loose connection with danger (Pattyn, Neyt, Henderickx, & Soetens, 2008). This would be the case in studies, say, investigating factors that affect the ability to maintain concentration during tedious monitoring tasks on a computer screen. In the scientific literature dealing with the behaviour of non-human animals, vigilance relates to the monitoring of threats be they caused by predators or conspecifics (Beauchamp, 2015) (Box 1). This is similar to the definition used by psychologists except that they use the label “risk assessment” to describe the behavioural patterns associated with the detection of threats or the increased watchfulness that follows the detection of such threats (D. C. Blanchard, Griebel, Pobbe, & R. J. Blanchard, 2011).

Vigilance can be a behaviour or a state, and obviously most field studies have focused on documenting external markers of vigilance such as head position. For example, vigilant
animals will raise their heads from the ground to scan the surroundings. An internal state of vigilance could be inferred using empirical data about the ability to detect threatening stimuli (Dimond & Lazarus, 1974), but there has been little work in that direction. One problem of using external markers to infer vigilance is that animals could be in a vigilant state (thus able to detect threats) without showing clearly observable signs of vigilance. This would be the case, say, for rats looking down at food but still able to scan the area above their heads using their lateral eyes (Wallace et al., 2013). Conversely, an animal could be in a non-vigilant state (unable to detect threats) and yet adopt a vigilant posture. For instance, individuals who are seemingly vigilant for threats can actually be searching for food. Another issue is that vigilance is difficult to measure in species such as insects and fish where external signs of vigilance are not obvious (to us).

**Box 1. Glossary**

**Antipredator vigilance:** Monitoring of threats related to predators.

**Fear:** For ecologists, fear represents what animals probably experience when facing threats by predators and conspecifics. In humans, fear is typically viewed as the conscious feeling that arises when threatened. More generally, fear can be viewed as a state that links threatening stimuli to the set of responses to such threats including physiological and behavioural changes.

**Landscape of fear:** Expression coined by ecologists to indicate that the risk posed by predators can vary both in time and in space in the habitat of an animal.

**Pre-emptive vigilance:** Vigilance to detect signs of predator activity or signs that neighbors are threatening before they actually launch their attacks.

**Reactive vigilance:** Vigilance aimed at present threats.

**Social vigilance:** Monitoring of threats related to conspecifics.

**Threat:** Any cue that signals a potential attack.

**Vigilance:** Monitoring of potential or actual threats using different sensory modes (e.g., visual, auditory). Typically, vigilance involves the cessation of ongoing activities to monitor the surroundings for danger. This monitoring can involve several behavioural patterns depending on the species, including movements of the head to bring different areas into visual focus, sniffing, and reorientation of the ears.

In addition to potentially low sensitivity and specificity (Figure 2), it is also not always easy to detect the target of vigilance. Animals can maintain vigilance to detect predators, the so-called antipredator vigilance, or to detect potentially aggressive conspecifics, the so-called social vigilance (Hall, 1960) (Box 1). Animals can use the same posture for both types of vigilance, making it hard to distinguish between the two. In animals with forward-facing eyes, the direction of the gaze could be used to infer the target of vigilance: if the animal looks away from the group, then vigilance is probably aimed at predators, while glances at nearby conspecifics probably betray social vigilance (Favreau, Goldizen, & Pays, 2010).

The hallmark of vigilance is that it is costly to perform (Lima & Dill, 1990). As in the sandpiper example above, time spent vigilant detracts from the ability to obtain food or to rest, which can translate into poorer future reproductive success. To mitigate such costs, competing activities can overlap. For instance, vigilance can be maintained during food processing, thus reducing the time during which no food can be obtained (Cowlishaw et al.,
2004). But even then, performing two activities at the same time might lead to suboptimal detection or food processing.

In general, it is fair to infer a higher level of risk from predators or from conspecifics when animals spend more time vigilant. Here are some examples with sandpipers. Falcons pose a greater threat when they can launch their attacks closer to shore because sandpipers have less time to detect and react to their fast approaches. Therefore, sandpipers devote more time to antipredator vigilance when they are closer to shore (Beauchamp, 2014a). Similarly, conspecifics pose a greater threat when they are closer, and sandpipers are more vigilant when neighbours are closer (Beauchamp, 2016b).

Vigilance can be pre-emptive or reactive. During pre-emptive vigilance, animals maintain vigilance to detect signs of predator activity or signs that neighbors are threatening before they actually launch their attacks. Reactive vigilance is concerned with the actual monitoring of threatening predators or conspecifics. Reactive vigilance provides the time necessary to assess the level of threat caused by a predator or a conspecific, and to choose a proper course of action such as fleeing or fighting. Some researchers propose that fear is associated with imminent threats and thus with reactive vigilance, while pre-emptive vigilance might be associated with anxiety because the threat is not imminent (Boissy, 1995; Bouton, Mineka, & Barlow, 2001). This classification scheme for vigilance is similar to the one that psychologists use to distinguish between potential, distal, and more proximal threats (R. J. Blanchard, Flannelly, & D. C. Blanchard, 1986; Fanselow & Lester, 1988; Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015).

Sociality has emerged as a key factor influencing both social and antipredator vigilance. Opportunities for competition typically increase with group size, and the expectation is that social vigilance increases with group size (Beauchamp, 2001; Treves, 1999). By contrast, the need for antipredator vigilance is expected to decrease in larger groups. This is because more eyes and ears are available to scan the surroundings for signs of danger, which enables individuals to relax their own vigilance at no increased risk to themselves (Pulliam, 1973). In addition, the risk of capture of any individual is diluted by the presence of more targets for the predator in a large group (Bertram, 1978). Better detection and risk dilution are the two main factors that allow antipredator vigilance to decrease in larger groups (Roberts, 1996).

To ensure that they are not left behind during an attack, individuals who have not detected a threat by themselves must be able to react rapidly to signs of alarm provided by neighbours (Lima, 1995). This collective detection implies that individuals can quickly assess cues or signals provided by alarmed neighbours. Signals like alarm calls are easy to detect and allow fast collective detection. Indirect cues of alarm are also available such as noisy takeoffs (Cresswell, Hilton, & Ruxton, 2000; Hingee & Magrath, 2009) or interruptions in feeding suggesting that a threat is currently monitored (Pereira, Cruz, Lima, & Moita, 2012). Cues that are familiar to us like facial expressions of fear can be recognized by some animals (Tate, Fischer, Leigh, & Kendrick, 2006).

It was long thought that animals adjusted their vigilance independently from one another (Pulliam, 1973), but recent work suggests that they actually pay attention to the vigilance of their neighbours (e.g., Beauchamp, 2009; Ge, Beauchamp, & Li, 2011; Pays et al., 2007; Podgórski et al., 2016). This can be useful when animals need to coordinate or synchronize their vigilance. Coordination ensures that a more constant level of vigilance is maintained at the group level, and it implies that animals avoid being vigilant when others
Synchronization occurs when individuals in the group tend to become vigilant at the same time. Coordination and synchronization of vigilance imply that animals can recognize that others are vigilant, and act accordingly.

Some researchers have suggested using vigilance as a measure of fear (Welp, Rushen, Kramer, Festa-Bianchet, & de Passillé, 2004) or more generally as an indicator of welfare (Mason & Veasey, 2010). Ecologists also propose that fear underlies predation risk (Blumstein, 2006; Brown, Laundré, & Gurung, 1999; Gallagher, Creel, Wilson, & Cooke, 2017; Gil, Emberts, Jones, & St. Mary, 2017; LaManna & Martin, 2016; Laundré, Hernandez, & Altendorf, 2001; Laundré, Hernandez, & Ripple, 2010; Preisser, Bolnick, & Benard, 2005; Stankowich & Blumstein, 2005), which makes a strong case for using vigilance as a measure of fear because of its strong association with the level of perceived risk. Measurements of vigilance are relatively easy to make and non-invasive, rendering them suitable for a quick evaluation of internal states. The extent to which fear can be inferred from vigilance is explored below.
3. Relationship between vigilance and fear

In its everyday meaning, “fear” is the conscious feeling that arises when facing a threat (Box 1). For ecologists, fear represents what animals probably experience when facing threats by predators and conspecifics. The emphasis is on “probably” because it is not clear whether non-human animals experience feelings of fear just as humans do. More generally, fear can be viewed as an internal state that links threatening stimuli to the set of responses to avoid such threats including physiological and behavioural changes (Adolphs, 2013). These responses include more vigilance and a host of physiological responses including the release of stress hormones and an increase in heart rate. Neuroscientists have identified neural circuits in the brains of mammals that are involved in the production of responses to threats (Gross & Canteras, 2012; Lang, Davis, & Öhman, 2000; McNaughton & Corr, 2004; Mobbs et al., 2015; Pellman & Kim, 2016). Stimulation of these brain areas produces behavioural and physiological responses that are similar to those observed when animals face a threat. In addition, lesions to these brain areas greatly impair the production of these responses.

That vigilance betrays fear is often posited in the literature especially when it comes to antipredator vigilance (Blumstein, 2006; Brown et al., 1999; Gallagher et al., 2017; Laundré et al., 2001; Laundré et al., 2010; Stankowich & Blumstein, 2005). Fear in this case is thought to reflect predation risk. The “landscape of fear,” for instance, describes how fear varies both in space and in time in the habitat where prey animals live. The distance between sandpipers and obstructive cover, from which falcons launch their attacks, is one example of a landscape feature associated with predation risk and thus (presumably) fear. Notice that a more objective term could be used to describe variation in risk in a habitat such as “landscape of risk or danger.” I think it is fair to say that in most such cases, fear is assumed rather than measured.

The leap in logic here is that a higher predation risk translates into more fear, from which we would expect behavioural and other adjustments to reduce the chances of predation. This leap to the mental realm is rather atypical of students of animal behaviour, but can be explained by the continuity argument suggesting that animals, just like us, probably experience emotions (Bekoff, 2007), and that fear must be the emotion driving reactions to predators (and presumably conspecifics) such as vigilance and fleeing.

It has been argued that because fear cannot be easily measured, we cannot really infer that animals are in a state of fear and certainly not imply that animals are feeling fearful (LeDoux, 2014). Just consider the following example to illustrate the opposing viewpoints. Several studies have shown that a higher risk of predation can affect reproduction (Clinchy, Sheriff, & Zanette, 2013; Hawlena & Schmitz, 2010). One possible interpretation for this association is that predation risk causes fear and anxiety, and the resulting physiological consequences eventually affect reproduction. An alternative interpretation is that the stress is caused by other factors such as the low food intake that resulted from behavioural adjustments to higher risk, with no implication for fear at all (Creel, Winnie, & Christianson, 2009).

For ecologists, vigilance and other measures such as the distance at which animals flee from a threat (Cooper & Blumstein, 2015), represent an external marker of fear whose level tracks predation risk in a habitat. The link between predation risk and vigilance is so strong
that there can be little doubt that vigilance can be a very good marker of predation risk. Whether we accept vigilance as a marker of fear remains an open question.

How can we make a case for using vigilance as a marker for fear rather than simply assuming that vigilance betrays fear? In the laboratory, it is possible to infer fear from the activation of particular brain circuits involved in the response to threatening stimuli (Gross & Canteras, 2012). In the field, however, this option is not possible. One possibility that I explore below is to examine whether vigilance tends to co-occur with other measurable expressions of fear. Fear is usually associated with the expression of several measurable variables including vigilance (D. C. Blanchard et al., 2011), but also other physiological correlates such as heart rate and stress hormone release (Adolphs, 2013; Lang et al., 2000). If threatening stimuli triggered vigilance along with a host of other physiological responses typically associated with fear at the same time, the case for using vigilance as a marker of fear would be that much stronger. In the following, I examine the strength of the association between physiological correlates of fear and vigilance first in the context of predation and then in the context of threats caused by conspecifics.

3.1. Predation risk and fear

Countless studies have shown that exposure to a predator or to signs of predator activity increases levels of vigilance (e.g., Caraco, Martindale, & Pulliam, 1980; Creel, Schuette, & Christianson, 2014; Z. Li, Jiang, & Beauchamp, 2009; Périquet et al., 2012). Similarly, exposure to a predator or to indirect predator cues (like distance to cover for sandpipers) or to chronic predation risk over a longer period of time in a wide variety of taxa — from invertebrates to fish, birds, and mammals — can trigger a host of physiological responses compatible with a fear response including increased heart rate and release of glucocorticoids or stress hormones (Clinchy et al., 2013; Harris & Carr, 2016; Hawlena & Schmitz, 2010). Laboratory studies conducted with brief exposure to predators also show numerous endocrine and nervous responses (Gross & Canteras, 2012).

I first examine the association between vigilance and levels of stress hormones before considering other physiological correlates of fear. Stress hormone levels can be measured directly in the plasma or indirectly using fecal glucocorticoids (fGCs). I distinguish between reactive and pre-emptive antipredator vigilance to highlight the distinction between responses to immediate risk and responses to long-term exposure to risk, which would reflect a more chronic exposition.

3.1.1. Stress hormone production and reactive vigilance

Gun shots during hunting season provide a good example of an acute stressor that reflects a sudden increase in predation risk. Gun shots triggered an increase in fGCs in fallow deer (Dama dama) that lasted only a few days. As expected, deer vigilance increased in areas where culling occurred (Pecorella, Ferretti, Sforzi, & Macchi, 2016). However, the increase in vigilance was reported over a much longer period than the short-lived hormonal response, suggesting that higher vigilance persisted despite low levels of stress hormones. A tighter coupling between fGCs and vigilance was documented in little bustards (Tetrax tetrax) subjected to varying levels of hunting pressure during the same week (Tarjuelo et al., 2015). Bustards showed elevated levels of fGCs and higher vigilance on weekends, when hunting pressure was highest, but less so before and after. Elevated levels of fGCs can also be associated with other factors besides perceived predation risk including food challenges and
social instability (Sapolsky, Romero, & Munck, 2000), but the contribution of these factors was not explored.

Rabbits (*Oryctolagus cuniculus*) exposed to fox odours showed increased vigilance. Parallel changes in serum GCs occurred in confined conditions (Monclús, Rödel, Von Holst, & De Miguel, 2005), but not in a more open setting where rabbits could roam more freely (Monclús, Rödel, & von Holst, 2006). Other studies failed to document concomitant changes in stress hormones and behavioural responses other than vigilance when predation risk increased (Cockrem & Silverin, 2002; D. R. Davis & Gabor, 2015; Fonner & Woodley, 2015). One possible explanation of these findings is that stress hormone release is less likely when threats are more predictable or when animals have more control over the situation (Sapolsky et al., 2000). Therefore, stress hormone production and antipredator responses can conceivably be uncoupled.

### 3.1.2. Stress hormone production and pre-emptive vigilance

The previous section focussed on short-term exposure to predation risk. In other cases, animals are exposed to a certain level of predation risk over longer time spans. Vigilance in this case serves a pre-emptive purpose, as it is not directed at immediate threats.

Variation in group size is a convenient way to examine parallel changes in stress hormone production and vigilance. As pointed out earlier, animals in smaller groups are expected to allocate more time to antipredator vigilance. Higher predation risk in such groups, which is expected to translate into more fear, should thus trigger the release of stress hormones. In sheep (*Ovis aries*), cortisol production (a stress hormone) and vigilance peaked in the smaller groups (Michelena et al., 2012). Food stress could not be implicated in the production of cortisol, given that the amount of food available prevented competition.

An assumption here is that variation in group size only reflects variation in predation risk and thus in fear level. In the smaller groups, however, individuals are also isolated from one another. In species with strong bonds between group members, isolation from group mates is known to trigger the release of stress hormones (Hawkley, Cole, Capitanio, Norman, & Cacioppo, 2012). Even within the confines of a group, the loss of a companion is sufficient to release stress hormones (Engh et al., 2006). Similarly, isolated sheep who saw a familiar face on a screen released less cortisol (da Costa, Leigh, Man, & Kendrick, 2004).

Uncoupling between stress hormone release and vigilance is not unusual after separation. For instance, ravens (*Corvus corax*) recently isolated from the flock became less vocal and spent more time feeding (less vigilance) over time despite little changes in fGCs during the separation period (Munteanu, Stocker, Stöwe, Massen, & Bugnyar, 2017). By contrast, the level of cortisol in cows decreased as individuals experienced repeated separations despite little changes in vigilance (Müller & Schrader, 2005).

The above discussion illustrates one of the difficulties in using physiological markers to assess the underlying fear state in that such markers are not always specific to fear. In the sheep example, separation anxiety as well as increased fear due to greater predation risk in smaller groups can both explain the observation that vigilance and stress hormones levels are higher in smaller groups. Perhaps one way to tease apart these two distinct phenomena is to determine the target of vigilance in smaller groups. Any signs that attention is devoted to searching for group mates rather than scanning for predation threats would suggest that increased predation risk might not be the only factor that triggers the release of stress hormones in smaller groups.
Other studies have taken advantage of natural variation in individual vigilance levels. A link between pre-emptive vigilance and fGCs was investigated in meerkats (*Suricata suricatta*). In this species, individuals who excreted more GCs exhibited higher vigilance (Voellmy, Goncalves, Barrette, Monfort, & Manser, 2014). It is not clear, however, if other factors contributed to this association. For instance, more active individuals who naturally excrete more GCs could also be more vigilant (Clary et al., 2014). Similarly, if more vigilant individuals are in a poorer state due to more restricted feeding, higher levels of fGCs could arise as a consequence of reduced food intake rather than predation risk.

In species of rodents in the field, it appears that the reverse pattern applies in that more vigilant foragers showed lower levels of fGCs (Chmura, Wey, & Blumstein, 2016; Mateo, 2007). Predictability in predation risk in one of these species was thought to explain low levels of fGCs, which would be boosted in the case of an attack (Mateo, 2007). An alternative explanation is that chronic exposure desensitized individuals, leading to low levels of stress hormone production despite high risk and high vigilance. There could also be costs to maintaining a high level of stress hormones over a long period of time, implying that selection would favour a quicker return to more normal values despite high risk (Boonstra, 2013).

Reintroduction of wolves (*Canis lupus*) to the Greater Yellowstone Park area provides a golden opportunity to see how spatial variation in predation risk affects elk (*Cervus elaphus*) reproduction and antipredator behaviour (Laundré et al., 2001). The threat of predation by wolves has led to a decrease in reproduction in elk and also to a decrease in population size (Creel, Chrisianson, Liley, & Winnie, 2007), which implies that wolves can have a significant impact on elk demography. As expected, vigilance in areas with higher predation risk substantially increased (Liley & Creel, 2008). However, fGCs did not track the level of predation risk measured by the researchers (Creel et al., 2009), suggesting that the demographic effects noted above were not associated with the perception of fear, but rather with changes in other ecological variables such as food intake. Nevertheless, one would expect food shortages to increase levels of fGCs, which was not the case here, casting doubt on this interpretation (Boonstra, 2013). These results led the researchers to raise the possibility that predation risk can have an impact on vigilance and other variables without involving the fear response, which means that elk might not fear wolves after all even though they make choices to reduce predation risk.

Other studies have not reported vigilance but have shown a stronger association between GCs and predation risk (Monclús, Palomares, Tablado, Martínez-Fontúrbel, & Palme, 2009; Sheriff, Krebs, & Boonstra, 2011), although this seems to vary depending on the species (Ylönen, Eccard, Jokinen, & Sundell, 2006). Generally, the association between GCs and acute or chronic predation risk is not always strong, as only a fraction of studies, from 38% to 77% depending on the taxa, have documented an increase in cortisol following exposure to predation risk (Harris & Carr, 2016). Several factors might explain uncoupling of predation risk and stress hormone levels including individual variation, low predation risk, and habituation in the case of chronic exposure (Harris & Carr, 2016). While these factors can help us understand why stress hormone release might not be activated, it is still the case that predation risk can trigger adjustments in vigilance despite little changes in stress hormone release.

Exposure to anthropogenic sources of disturbances such as traffic, noises or visitors has long been known to affect vigilance (see Beauchamp, 2015, for a review). If such disturbances cause fear and a subsequent increase in vigilance, one might expect GC levels to
be higher in more disturbed situations. For instance, a clear association has been documented between snowmobile activity and fGCs in elk and in wolves (Creel et al., 2002). In free-range exhibits with kangaroos (Macropus giganteus), an increase in visitor numbers led to higher vigilance but fGCs remained at the same level (Sherwen, Hemsworth, Butler, Fanson, & Magrath, 2015). In this particular case, it is possible that visitors were considered a source of curiosity rather than disturbance, and/or that access to refuges in the exhibit dampened the stress response. In Magellanic penguins (Spheniscus magellanicus) exposed repeatedly to simulated visits by tourists, the number of head turns, a measure of vigilance, decreased over time in parallel to a decrease in GC secretion (Walker, Boersma, & Wingfield, 2006), suggesting a closer coupling between behavioural changes and stress hormone production.

The above studies are observational in nature, which often complicates the interpretation of the results given that several uncontrolled factors can influence the outcome of interest. A few studies used an experimental approach instead, and documented changes in vigilance in response to the administration of GCs like cortisol. In meerkats, experimental injection of cortisol did not increase vigilance behaviour (Santema, Teitel, Manser, Bennett, & Clutton-Brock, 2013), although it led to a decrease in feeding. Similarly, injection of cortisol failed to alter vigilance in Adélie penguins (Pygoscelis adeliae) on the nest (Thierry, Brajon, Spée, & Raclot, 2014) and in barn owl (Tyto alba) chicks (Dreiss et al., 2013). Because hormone levels are kept at high levels over a relatively long period, these studies can only address responses to rather chronic exposure. Other experimental studies showed that vigilance increased in animals exposed to chemicals that induce anxiety (Sapolsky & Share, 2004) or decreased in animals exposed to calming agents (D. C. Blanchard, Griebel, & R. J. Blanchard, 2001; Choy, Yu, Hawkes, & Mayorov, 2012). However, the target of vigilance in these studies could not be pinpointed.

Summing up, the rather conflicting results presented here suggest that some species might only show a response to acute predation risk (sudden apparition of a predator or detection of predator cues) while others mount a long-term reaction that is evidenced by a positive relationship between GCs and vigilance (Boonstra, 2013). But overall, the association between vigilance and stress hormone release is rather weak.

3.1.3. Vigilance and other markers of fear

The previous discussion focussed on one possible marker of fear, namely, the production of stress hormones. Given that stress hormone production is not always specific to the perception of risk, it is important to consider other potential physiological correlates of fear. Fear responses can involve several other variables. In particular, within seconds following the perception of a threat, a series of physiological responses come into play including changes in heart rate, respiratory rate, and also pupil size (Charmandari, Tsigos, & Chrousos, 2004). These changes can be considered physiological correlates of fear at the acute level.

In several species of birds and mammals, rapid increases in heart rate following the detection of a threat closely matched intense bouts of vigilance even without concomitant changes in physical activity (Christensen, Keeling, & Nielsen, 2005; Christensen, Malmkvist, Nielsen, & Keeling, 2008; Ellenberg, Mattern, & Seddon, 2013; Ely, Ward, & Bollinger, 1999; Holmes, Giese, & Kriwoken, 2005; Karpovich, Skinner, Mondragon, & Blundell, 2015; MacArthur, Johnston, & Geist, 1979), suggesting that increased vigilance and heart rate adjustments are correlated responses following the perception of acute risk. However, there are cases where rapid changes in heart rate following the perception of a threat occurred
without a notable change in vigilance (Ellenberg, Mattern, Seddon, & Jorquera, 2006; Giese, 1998). It is perhaps the case that vigilance was not clearly recognized in these studies or that the risk was too low to alter vigilance appreciably. More generally, it should be pointed out that since vigilance is costly to perform, the lack of an adjustment in vigilance in response to a threat, which might be indicated by other markers of fear like heart rate, might indicate that animals cannot afford to be vigilant despite fear. This could be the case for animals who are very hungry or who lack access to alternative foraging areas (Gill, 2007).

In other studies, the reverse was true in that changes in vigilance occurred following the detection of a threat without changes in heart rate (Christensen & Rundgren, 2008; Dielenberg, Carrive, & McGregor, 2001; Edgar, Paul, Harris, Penturn, & Nicol, 2012; Herskin, Munksgaard, & Kristensen, 2003). Similarly, domestic goats exposed to a threatening situation (novel person or another goat) produced many bleats suggestive of alarm and yet showed no changes in heart rate (Lyons & Price, 1987). These results suggest that in some species, vigilance or other external markers of fear can be altered without changes in heart rate. One possibility here is that the threat is not really a source of fear but of curiosity, which means that the threat should be relabelled as innocuous.

Pupil dilation has been viewed as an indicator of increased vigilance and attention following the perception of a threat (Ebitz, Pearson, & Platt, 2014). Accordingly, pupil size as well as vigilance rapidly increased in peacocks (Pavo cristatus) exposed to a predator model (Yorzinski & Platt, 2014). While an increase in pupil size is thought to reduce overall visual acuity, it might also allow individuals to focus their attention on predator movement and high contrast features of the predator, thus allowing them to tune out irrelevant features (Ebitz et al., 2014). Typical measurements of vigilance, like those from a time budget analysis, emphasize the quantitative nature rather than the qualitative value of vigilance. Changes in pupil size could thus be viewed as an adjustment in vigilance quality in response to the detection of a predation threat.

The perception of fear in humans leads to several changes in the configuration of the face, including eye widening and rapid eye movements, which can be interpreted as aiding the visual perception of threats (Susskind et al., 2008). Exposure to a predator also caused a decrease in blink rate in peacocks that would allow reducing the amount of time during which visual processing cannot be performed (Yorzinski, 2016). All these changes show that an acute stressor can affect not only the quantity but the quality of vigilance.

Overall, as was the case for stress hormone release, the relationship between vigilance and other markers of fear is not always strong, although qualitative changes in vigilance during short-term exposure to risk appear to correlate well with higher predation risk.

3.2. Social risk and fear

Predators are but one source of vigilance for animals. For species who live in groups, conspecifics can also be an important target of vigilance. Individuals in groups face attacks or threats by conspecifics over food or mates. Monitoring potentially aggressive conspecifics is thus expected to be important to reduce the impact of aggression. The social environment of an individual has long been associated with the release of stress hormones (Cavigelli & Caruso, 2015; Creel, Dantzer, Goymann, & Rubenstein, 2013; Tamashiro, Nguyen, & Sakai, 2005). In addition, there appears to be separate neurological pathways for fear associated with aggressive conspecifics and predators (Gross & Canteras, 2012). What is the evidence for an association between vigilance and the release of stress hormones in a social context?
In one monkey species, subordinates spent more time vigilant and showed higher levels of cortisol than more dominant group members, suggesting that being subordinate increased stress and that social vigilance betrayed fear of attacks (Shively, 1998). Because dominant group members could not really be avoided in the confined setting of the laboratory, it is not clear whether such results would extend to the field where individuals can presumably deploy more tactics to avoid aggressive encounters. Other laboratory studies in monkeys have also documented higher levels of cortisol in subordinates, but vigilance was not reported (Abbott et al., 2003; Coe, Franklin, Smith, & Levine, 1982).

Field studies with other species confirm some of these findings. Dominant, male, white-faced capuchin monkeys (Cebus capucinus), who are vulnerable to attacks from outsider males, showed both elevated fGCs and higher vigilance (Schoof & Jack, 2013). During the reproductive season, dominant males, who are also vigilant to guard females against rival males from the same group, also showed the highest levels of fGCs (Schoof, Jack, & Ziegler, 2014).

In many species, the position of an individual in the group, whether at the centre or at the periphery, influences predation risk and the intensity of competition with neighbours (Hirsch, 2007; Krause, 1994). Indeed, individuals at the centre of their groups are buffered to a greater extent from predation, but often face more competition from close neighbours. Central individuals should thus allocate more time to social vigilance, and if stress from conspecifics exceeds the stress from predators, they should also show higher levels of GCs. Forest baboons (Papio anubis) who occupied more central positions showed higher levels of fGCs (Tkaczynski, MacLarnon, & Ross, 2014). However, the level of vigilance was not correlated with fGCs in these baboons. In other species of monkeys, males in more central positions also showed higher levels of fGCs, but vigilance was not noted (Mendonça-Furtado et al., 2014; Van Belle, Estrada, Ziegler, & Strier, 2009). However, in a previous study of one of these species, dominant group members maintained more vigilance (Treves, Drescher, & Ingrisano, 2001), suggesting a link between social vigilance and stress hormones in this species related to spatial position.

High levels of GCs are not always found in subordinate group members as noted above in capuchin monkeys and also in other species (Creel, 2001). In groups of ring-tailed lemurs (Lemur catta), for instance, the highest levels of fGCs occurred in the dominant females (Cavigelli, Dubovick, Levash, Jolly, & Pitts, 2003). For the lower-ranking females, being attacked and occurring closer to one another best predicted increased levels of fGCs, which supports the idea that close neighbours can cause stress when they are potentially dangerous. In another study of the same species, dominant females showed the highest vigilance (Gould, Fedigan, & Rose, 1997), supporting a link between social vigilance and GC production.

In one monkey species, by contrast, GC production was lowest in the more vigilant group members during the mate-guarding season, a period during which males invest much time to guard females and monitor rival males (Girard-Buttoz, Heistermann, Rahmi, Agil, Ahmad Fauzan, et al., 2014). Since high vigilance and mate guarding are less likely when food is scarce, it is perhaps the case that low GC production reflected greater food availability, which itself allowed more vigilance and mate guarding.

There have been fewer studies involving taxa other than primates. In greylag geese (Anser anser), paired males with offspring during the reproductive season maintained more vigilance and showed higher levels of fGCs than paired males without offspring and unpaired
males (Kotrschal, Hirschenhauser, & Möstl, 1998). However, the target of vigilance could not be determined in this species.

Stress hormone release can clearly be related to social factors, but it can also be sensitive to a host of unrelated factors such as physical exertion, disease, and food challenges (Cavigelli & Caruso, 2015). To isolate threats by conspecifics as a factor responsible for stress hormone release, it is necessary to exclude these other contributing factors. This is especially relevant for subordinate group members who often have less access to resources or who occupy peripheral positions more exposed to predation (Hirsch, 2007). In addition, monitoring rivals takes time, and it may follow that stress hormone release reflects a negative energy budget rather than fear (Girard-Buttoz, Heistermann, Rahmi, Agil, Ahmad Fauzan, et al., 2014).

What could cause elevated levels of stress hormones in dominant group members, given that they are the ones initiating attacks? Perhaps stress comes from the fighting itself or the anticipation of future conflicts. Instability in the dominance structure of a group can also impose stress on dominant group members because aggressive encounters are more frequent (Setchell, Smith, Wickings, & Knapp, 2010). This suggests that stress can be in part a consequence of increased physical exertion. Another possibility is that by investing more time in vigilance to monitor neighbours, dominant group members experience a food shortfall, which on its own could explain the increase in stress hormone release (Girard-Buttoz, Heistermann, Rahmi, Agil, Fauzan, et al., 2014; Surbeck, Deschner, Weltrung, & Hohmann, 2012). In this case, it would be necessary to monitor food intake to see if vigilance really causes a decrease in food intake over the long-term.

The recognition of threats caused by other group members is so important that at least in primates several types of neurons are activated by subtle signs made by potentially aggressive individuals including gaze direction, body direction, and facial expression (Emery, 2000). Such neurons are located in one brain area that is in direct contact with the amygdala, a small structure at the base of the brain. It is the amygdala that attaches an emotional connotation to the firing of these specialized neurons, which would trigger fear and other physiological consequences (M. Davis, 1992; Pellman & Kim, 2016; Sander, Grafman, & Zalla, 2003).

The amygdala has been viewed as the key area of the brain dealing with fear and anxiety. Electrical stimulation of different parts of the amygdala produces many of the physiological and behavioural consequences associated with fear such as facial expression of fear, elevated heart rate, corticosteroid release, and vigilance (M. Davis, 1992; Pellman & Kim, 2016). Lesions to this structure disrupt judgments about facial features (Dal Monte, Costa, Noble, Murray, & Averbeck, 2015), which would make it more difficult to activate proper psycho-physiological reactions. The amygdala can thus be viewed as responsible for monitoring the environment for threats and directing the senses in acquiring further information (Whalen, 1998). The end result of these processes is often increased vigilance and a sharpening of the senses (Hermans, Henckens, Joëls, & Fernández, 2014; Shackman, Maxwell, McMenamin, Greischar, & Davidson, 2011) like we saw earlier with changes in pupil size and eye movements.

Oxytocin is known to attenuate responses in the amygdala, and in a recent study, injection of this hormone suppressed vigilance directed at other group members (Ebitz, Watson, & Platt, 2013), supporting the idea that the amygdala modulates the acquisition of information about social threats, and produces responses such as vigilance to such threats.
3.3. Perception of fear in others
Solitary individuals can only rely on themselves to acquire information about possible threats. In group-living species, other group members can act as a source of information about threats. Can social animals decode information from the reaction of neighbours to potential threats? If neighbours can pick up information from alarmed conspecifics, then alarm must be associated with cues that can be used to infer fear.

Upon detection of a threat, many species of animals produce signals to alert others. Typically, these signals take the form of alarm calls, which are known to trigger an immediate defensive reaction in nearby companions (Blumstein & Armitage, 1997; Seyfarth, Cheney, & Marler, 1980). What is less known is whether more subtle cues of alarm, such as visual fright reactions, can also convey information about threats to others. This raises the question as to whether animals can recognize fearful behavioural cues (other than alarm calls) in others and alter their own allocation of time to vigilance in response.

At least in humans, lesions to the amygdala increase the difficulty in recognizing fearful faces (Whalen, 1998). This is quite relevant because it indicates that we have the ability to recognize fear in others by facial expressions and direct our attention (increased vigilance) to discover the source of the threat. Lesions of the amygdala also make it more difficult to interpret faces showing surprise (Adolphs, Tranel, Damasio, & Damasio, 1994). In such faces, the eyes are opened wider, which as we saw earlier might be a means of acquiring more visual information. The intact amygdala would recognize that eye widening betrays the need to acquire more information about potential threats, and initiate the same response in the viewing subject.

In apes and monkeys, who are able to some extent to modify the configuration of their faces, the ability to recognize fearful facial expressions has been demonstrated in many species (Tate et al., 2006). More recent work also shows that other species with more rigid facial expressions, such as sheep, can produce different facial expressions following a threat (Greiveldinger, Veissier, & Boissy, 2009). In addition, sheep can also distinguish between fearful and calm facial expressions in others (Tate et al., 2006).

The ability to decode facial expressions or other reactions to threats is an important step, but the key question is whether animals who view such displays engage in more vigilance in response, which would demonstrate that these reactions in others are interpreted as a sign of fear. The evidence is rather limited at the moment. In rats, the cessation of foraging by one individual (a sign of vigilance) following a threat caused an increase in the vigilance of a neighbour who could not see the threat directly (Pereira et al., 2012). Similarly, female kangaroos (Macropus giganteus) who detected a snake nearby provided behavioural cues that induced a rapid increase in vigilance in nearby females prevented from seeing the snake (Pays, Beauchamp, Carter, & Goldizen, 2013). Naive pigs exposed to companions who showed more vigilance and other behavioural signs in anticipation of a negative outcome became more vigilant themselves than when exposed to more relaxed companions (Reimert, Bolhuis, Kemp, & Rodenburg, 2015). By contrast, in chickens (Gallus gallus), signs of fear in a companion failed to elicit more vigilance in observers despite the fact that observers themselves reacted with increased vigilance when they were exposed to the threat (Edgar et al., 2012). Perhaps in this case reactions would have been stronger if the threat was more obviously related to predation risk or if more neighbours became alarmed.
Another body of research shows that in many species of birds and mammals, individuals can synchronize their vigilance (e.g., Beauchamp, 2009; C. Li, Beauchamp, Wang, & Cui, 2016; Pays et al., 2007; Podgórski et al., 2016). That synchronization reflects copying of vigilance, rather than the independent detection of a threat by all group members, comes from the observation that synchronization takes place despite the lack of (obvious) external disturbances. It might be objected that vigilance synchronization only shows that animals copy the behaviour of their neighbours without necessarily copying the state of fear associated with that vigilance. For instance, people often eat more in the presence of others than when they are alone, without necessarily reporting feeling hungrier prior to the meal (Decastro & Brewer, 1992). Similarly, people who yawn in response to yawning by others are not necessarily tired (Bartholomew & Cirulli, 2014). A next step then would be to document rapid changes in other traits associated with fear, such as changes in heart rate or pupil dilation, during the synchronization of vigilance.

3.4. Vigilance and the feeling of fear

Fear as a state can be objectively measured with variables such as heart rate and the release of stress hormones. The feeling of fear, however, is more difficult to assess. The question of feeling concerns the awareness of the state of fear. No models of the optimal allocation of time to social or antipredator vigilance make any assumption about the feeling of fear (Beauchamp, 2017; Bednekoff & Lima, 2004; Lima, 1987; McNamara & Houston, 1992; Pulliam, 1973). Such models are concerned with the pattern of behaviour predicted to achieve the aim embodied in the model such as maximizing future expected reproductive success. Whether animals experience a feeling of fear is thus not an issue. Nevertheless, as we are dealing with fear, and as we know from our own experiences what fear feels like, it is interesting to wonder how much awareness is involved in the fear response, and ultimately whether other animals also experience such feelings.

Fear could not be induced or experienced (based on self-reporting) in a human subject with extensive lesions of the amygdala (Feinstein, Adolphs, Damasio, & Tranel, 2011). Obviously, the difficulty is that self-reporting cannot be done with non-human subjects. Nevertheless, is there any indication in humans that the state of fear can be induced unconsciously? In one study, the amygdala responded to subliminal (undetectable visually) pictures of fearful faces (Jiang & He, 2006), suggesting that awareness of the threatening stimuli is not essential to trigger fear responses. This and other studies suggest a rapid pathway to the amygdala before we even become aware of the stimuli eliciting fear (Mendez-Bertolo et al., 2016). Future studies could investigate the possibility that relevant threat stimuli other than fearful faces are processed similarly in humans and other species.

It is one thing to be unaware of the threatening stimuli, but is it possible to be in a state of fear without consciousness of the fear itself? Humans seeing scrambled fearful faces (hard to recognize) showed increased responses in the amygdala and yet reported little fear (Whalen, 1998). The concept of unconscious emotion is quite controversial (Berridge & Winkielman, 2003). It would mean, for instance, that an individual allocates more time to vigilance after the perception of threatening stimuli (with or without awareness) and that the treatment of that information, leads to an observable change in behaviour but without the feeling of fear. Some argue that studies about the feeling of fear are best left to humans, although feelings of fear are not excluded \textit{a priori} in non-human animals (LeDoux, 2014). The
point is well-taken that mechanisms that lead to vigilance through the neural pathways mentioned earlier might be different from those that cause the feeling of fear.

4. Discussion

The framework that I presented here contains the following elements. Threats, be they direct (an approaching predator or a threatening conspecific) or indirect (features of the physical and social environment of an animal associated with a higher risk) elicit reactive or pre-emptive vigilance along with a host of physiological reactions including rapid adjustments and more delayed responses (Figure 3). I sought a link between vigilance, a putative behavioural marker of fear, and well-established physiological correlates of fear such as heart rate increases and stress hormone release.

The results are mixed: several studies reported a positive association between vigilance aimed at predators or at conspecifics and physiological correlates of acute or chronic risk, but many others documented no such association or even a negative association. Lack of association with other correlates of fear for both reactive and pre-emptive vigilance is unexpected under the hypothesis that vigilance betrays fear. Based on the findings reported previously, I now consider various cases for the association between vigilance and physiological correlates of fear, and what they imply for the question that I tackle here, namely, what does vigilance tell us about fear?

Case 1: a threat induces an increase in vigilance with concomitant changes in at least one of the physiological correlates of fear. In such cases, vigilance would be a good marker of fear. One issue here is to ensure that the target of vigilance has been identified correctly. If the goal is to demonstrate that vigilance betrays fear of predation, for instance, it should be possible to demonstrate that vigilance was effectively aimed at predators.

Case 2: a threat fails to increase vigilance despite changes in at least one of the physiological correlates of fear. In this case, vigilance is a poor marker of fear. The simplest explanation for the lack of association hinges on the sensitivity of external markers of vigilance. Vigilance might thus have been underestimated or misidentified. A better understanding of the sensory basis of vigilance behaviour in our study animals will likely increase the sensitivity of our measurements (Fernández-Juricic, 2012) and reduce such mismatches with physiological states. Another explanation is that animals are really fearful, but are unable to allocate more time to vigilance. This might apply, for instance, to animals who are very hungry. Changing hunger levels by food supplementation or measuring the level of hunger might be ways to investigate this hypothesis.
Case 3: a threat induces an increase in vigilance but without concomitant changes in the physiological correlates of fear. One simple explanation for the lack of association is that vigilance betrays curiosity rather than fear. This could be investigated by using a different threatening stimulus or one that more closely matches the type of threats faced by the species. Another simple explanation is that the physiological correlates of fear have not been measured properly. If, for instance, the production of stress hormones fluctuates widely during the period of higher risk (Cavigelli & Caruso, 2015), more sampling might be needed to obtain a better estimate of the mean. Similarly, peaks in the production of stress hormones might be missed especially when sampling feces at irregular intervals.

Under chronic exposure to stress, stress hormone release often decreases over time (Cyr & Romero, 2009). Stress hormone release in particular can return to low values over time as a result of desensitization (inability to mount a response to any threat). Here, the animal can be fearful and vigilant despite low levels of stress hormones or little changes in other physiological correlates of fear. This hypothesis can be tested by measuring the
physiological response of animals to a different type of threat to see if they can mount a response at all.

Another mechanism that could produce an uncoupling of vigilance and physiological markers of vigilance is social buffering. Social buffering refers to the beneficial effect of conspecifics on the recovery after the experience of stress (Kikusui, Winslow, & Mori, 2006). The beneficial effects tend to go in the same direction for behavioural as well as physiological responses to threats, but it is not always the case. As an example, monkeys exposed to a snake when alone showed more agitation (movements and vocalizations) than when tested in pairs, and yet cortisol levels remained at the same level regardless of group size (Coe et al., 1982). If social buffering acts more strongly on the behavioural or the physiological markers of fear, an uncoupling of responses is possible.

A final case could be made that vigilance can be triggered despite no fear, which is reminiscent of the idea that animals make choices to reduce predation risk without the need to invoke fear (Creel et al., 2009). If vigilance is viewed as a reflex following stimulation of the neural circuits involved in the fear response, just as uncontrollable as the increase in heart rate or pupil dilation, then it would seem that vigilance could not occur without fear. However, if vigilance can be controlled rationally to achieve the goal of reducing the risk of attack, vigilance could take place without the involvement of the fear circuitry at all. The open question is whether there is any evidence in support of this conjecture.

**Case 4:** a threat induces no changes in vigilance as well as no changes in the physiological correlates of fear. If the threat is meaningful and if measurements of vigilance and of the physiological correlates of fear are sensitive enough, this scenario represents the worst case. It could be a sign that animals are desensitized after chronic stress and also unable to allocate more time to vigilance. Vigilance would be a poor marker of fear here as well.

Another possibility is that the threat is not meaningful (low risk), in which case it is futile to look for an association between vigilance and physiological correlates of fear. Alternatively, a threat can gradually lose its ability to trigger responses over time. With habituation, animals exposed repeatedly to a threat that fails to bring negative outcomes gradually respond less to the threat over time. By contrast to desensitization, habituated animals retain the ability to mount a response to other types of threats, and this could be used to distinguish the two phenomena. There are many examples of habituation to threats both for vigilance (see Beauchamp, 2015, for a review) and for stress hormone release (Cyr & Romero, 2009). Knowledge of the history of exposure to the threat over time is necessary to assess this hypothesis.

A final note concerns the existence of consistent individual patterns of responsiveness to stress (Boissy, 1995). Responses to stress might thus vary in a consistent manner (over time and contexts) in different individuals. For instance, subordinate baboons tend to show elevated levels of cortisol in the field, but there are subsets of subordinates characterized by peculiar behavioural patterns that produce cortisol at the same level as dominants (Virgin & Sapolsky, 1997). Because of this individual variation, cortisol levels would be more poorly associated with dominance status. Consistent differences in vigilance levels, with some individuals showing consistently high or low vigilance across contexts, have been documented in some species (Carter, Pays, & Goldizen, 2009; Couchoux & Cresswell, 2012; Dannock, Blomberg, & Goldizen, 2013; Favreau et al., 2014; Hoogland, Hale, Kirk, & Sui, 2013;
Mathot et al., 2011; Rieucau, Morand-Ferron, & Giraldeau, 2010; Roche & Brown, 2013), although this is not always the case (Pangle & Holekamp, 2010). Strong individual patterns of vigilance would decrease the association between fear and vigilance because vigilance is more poorly correlated with predation or social risk.

5. Conclusions

In view of the above considerations, vigilance might not always be a reliable indicator of the state of fear. This conclusion stems from the observation that vigilance is neither a totally sensitive nor specific marker of the vigilance state, and that other physiological markers of the state of fear are neither totally sensitive nor specific to that state.

With respect to the measurement of vigilance, a better understanding of its sensory basis would probably reduce the mismatch between markers of vigilance and the vigilant state. For example, measurements of visual acuity when animals adopt different postures can greatly increase our understanding of the limits of threat detection in animals and thus help us define vigilance more accurately (Fernández-Juricic, 2012). Vigilance carried out with other senses, such as ears and noses, is less likely to be influenced by postures. If vigilance using these other sensory modes is associated with reliable behavioural cues (e.g., sniffing or ear movements), it should be possible to see whether that can more accurately reflect the state of vigilance. Researchers can also pay more attention to the context in which vigilance is measured to eliminate some simple confounding factors such as hunger and habituation.

With respect to physiological correlates of the state of fear, the researcher could also pay attention to the context in which these measurements are made to reduce the impact of habituation or desensitization. Measurements of physiological correlates of fear are less likely to involve these two factors in the case of acute risk responses. Known confounding factors, such as food stress for the production of stress hormones, should be evaluated carefully when assessing responses.

Assessments of the fear state with indirect behavioural and physiological responses can also be improved by combining multiple responses to compensate for the relative lack of sensibility or specificity associated with each type of response. At some point, it might be relevant to ask which minimal set of behavioural and physiological correlates is needed to accurately pinpoint the state of fear. Other correlates of fear might also be considered in the future in addition to stress hormone release and heart rate. Earlier I mentioned changes in facial expressions and pupil size, but other simple variables could also be evaluated including respiration rate and body temperature (Edgar, Nicol, Pugh, & Paul, 2013; Vianna & Carrive, 2005). With proper adjustments, one can foresee that vigilance could actually tell us a lot about fear.

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Consciousness in teleosts: 
There is something it feels like to be a fish

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Abstract: Ray-finned fish are often excluded from the group of non-human animals considered to have phenomenal consciousness. This is generally done on the grounds that the fish pallium lacks a sufficiently expansive gross parcellation, as well as even minimally sufficient neuronal organization, intrinsic connectivity, and reciprocal extrinsic connections with the thalamus to support the subjective experience of qualia. It is also argued that fish do not exhibit the level of behavioral flexibility indicative of consciousness. A review of neuroanatomical, neurophysiological and behavioral studies is presented which leads to the conclusion that fish do have neurobiological correlates and behavioral flexibility of sufficient complexity to support the hypothesis that they are capable of phenomenal consciousness.

Keywords: comparative consciousness, phenomenal consciousness, fish, pallium, comparative anatomy, comparative behavior

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1. INTRODUCTION

Two connected theses will be defended in this paper. The first thesis is that ray-finned fishes of the teleost subclass (Actinopterygii; hereafter referred to simply as fishes)\(^1\) are sentient. The second thesis is that the pallium contributes to sentience in these species. Allen and Trestman (2016) equate phenomenal consciousness and sentience. I will adapt their use of the term and define sentience\(^2\) as at least the minimal capacity to have subjective experience of the qualities associated with external and internal sensations, as well as affective and motivational states. The consequence of this capacity is that there is something that it “feels like” to be the individual, human or animal, that has subjective experience (Nagel 1974).

I argue that there is something it feels like to be a fish. Others disagree, and usually ground their disagreement on two general arguments. The first argument is that fishes lack the neuroanatomical substrates necessary for consciousness. This argument assumes that a layered neocortex, or a structure homologous to it, with a number of anatomically distinct divisions and reciprocal anatomical connections among them, is required for even minimal sentience. Furthermore, massive reciprocal connections between the neocortex and the thalamus are needed. Because the fish pallium is not homologous to the mammalian neocortex, and its reciprocal connections with the thalamus are sparse, fishes lack the required neuroanatomical substrates for sentience (Cabanac et al. 2009; D. Edelman et al. 2005; Key 2015, 2016a; Rose 2002, 2007; Rose et al. 2012; Seth et al. 2005). The second argument follows naturally from the first. It is that fishes do not exhibit behaviors that require sentience. On this view, all of the behaviors observed in fishes, regardless of how complex they appear to be, are explicable by reference to simple sensory–motor reflexes, species-typical behaviors, or procedural/implicit learning and memory. I contend that both of these arguments fail.

In this target article I will present research supporting the hypothesis that the fish brain is neuroanatomically complex enough to support sentience. I will also present evidence that the pallium of the fish has neurophysiological activity similar to correlates of sentience in mammals. Finally, I will provide selected examples of behaviors generally thought to require sentience in humans.

2. SENTIENCE IN FISHES: THE OPTIC TECTUM

Several theories propose that sentience emerged in animals when the hindbrain, midbrain and diencephalic nuclei first evolved (e.g., Damasio 2010; Feinberg and Mallatt 2013, 2016; Merker 2007; Panksepp 2005). These theories differ in neuroanatomical detail and in the physiological and behavioral processes they emphasize. They will not be reviewed here (see Feinberg and Mallatt 2016, chapter 7, for a discussion). However, they have the following in common: (i) proposing that at least minimal sentience is possible without a neocortex, and (ii) attributing a role in the generation of sentience to the optic tectum.

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\(^1\) Cartilaginous fishes, such as sharks and rays, from the class chondrichtyans are not included in this discussion.

\(^2\) What I am calling sentience is, in general, the same process that Feinberg and Mallatt (2016) call sensory consciousness and that G. Edelman (1989) refers to as primary consciousness.
Figure 1. The drawings in this figure are provided as aids in visualizing the physical relationships among the major divisions of the fish brain discussed in the text. They are generalized representations and may therefore deviate in detail from the specific descriptions given in the cited references. (A) Schematic of a longitudinal (sagittal) section of the fish brain. The drawing represents a parasagittal section from the location of the dashed line in (B). That is, it comes from a location slightly away from the midline of the brain. Abbreviations: Cb – cerebellum; Ha – habenula; Hy – hypothalamus; OB – olfactory bulb; OT – optic tectum; Th – thalamus; P – pituitary; PgC – preglomerular complex. (B) A schematic cross section from the dorsal through the ventral surface of one hemisphere of the fish telencephalon. The section is drawn to represent the approximate anterior-posterior level of the brain demarcated by the vertical line in (A). It shows the locations of the pallial divisions given by Nieuwenhuys and Meek (1990). Abbreviations (all beginning with D refer to divisions of the pallium): DD – dorsodorsal; DMd – dorsomedial dorsalis; DLv – dorsomedial ventralis; DLD – dorsolateral dorsalis; DC – dorsalis centralis; DP – dorsalis posterior; VT – ventral (subpallial) telencephalon; DMv – dorsomedial ventralis.

The fish optic tectum (Figure 1A) is more involved in sensorimotor integration in fishes than its homolog, the superior colliculus, is in mammals. All sensory modalities present in any given teleost species, with the exception of olfaction, are represented in the tectum. However, visual input is especially strong and the tectum is generally viewed as the primary visual center in fishes (Feinberg and Mallatt 2013, 2016; Li 2016; Meek 1983). As such, the tectum is crucial for the transformation of visual input into directed, adaptive global motor
output. This transformation begins with the creation of an accurate point-by-point representation of visual space on the retina. Feinberg and Mallatt (2016) refer to this representation as sensory isomorphism. Retinal input to the tectum generates an isomorphic neural representation of visual space. Feinberg and Mallatt take it as axiomatic “that mental images are a part of primary, sensory consciousness and, therefore, contribute to “something it is like to be.” The neural representation of the world in the tectum is experienced subjectively as mental images. On my view, this is an important insight into what it means for a neural system to participate in the generation of sentience.

2.1 Tectal Neuroanatomy

But what evidence is there that the optic tectum is a crucial part of such a neural system? Others, in particular Feinberg and Mallatt (2013, 2016) and Merker (2007), have provided extensive reviews of this evidence. I will not replicate these reviews, but will provide a brief account of data indicating that the optic tectum, and its extrinsic and intrinsic connections, meet the requirements to be an anatomical substrate of sentience in fishes. I will discuss only the visual modality, but the basic organizational pattern also applies to the other sensory modalities represented in the tectum.

One requirement is that the visual world be accurately represented in the tectum. Isomorphic retinal input mediated by the excitatory neurotransmitter glutamate terminates primarily in the uppermost of the six neuronal layers of the tectum on the opposite side of the brain. Both anatomical and electrophysiological studies indicate that the pattern of termination reflects the accurate point-by-point visual representation of the world created on the retina (Nevin et al. 2010; Meek 1983; Venegas and Ito, 1983). Another requirement is modulation of the primary sensory pathways by intrinsic excitatory and inhibitory interneurons. Primary sensory input to the tectum can be amplified by positive feedforward and feedback circuits created by excitatory glutaminergic interneurons. Intrinsic inhibitory circuits created by interneurons that use γ-aminobutyric acid (GABA) as a transmitter provide for temporal stabilization and spatial sharpening of activity within the excitatory circuits (Kardamakisa et al. 2015; Nevin et al. 2010). One function of these inhibitory circuits may be to improve discriminability of objects in the fish’s visual field. Ablation of these neurons selectively impairs prey capture in zebrafish (Del Bene et al. 2010), possibly because the prey is perceived as larger than it is and because predator avoidance rather than prey approach behavior is selected (Barker and Baier 2015).

The tectum also receives input from mesencephalic and hindbrain nuclei, as well as the diencephalic and telencephalic regions, including the pallium. As will be discussed below, this input allows memory and emotion to influence tectal output to brainstem structures that regulate motor programs. The output of the tectum arises from neurons located in its deeper layers. This output terminates in the telencephalic, diencephalic, and brainstem sites that provide input to the tectum, and, most importantly, in premotor brainstem nuclei that directly control behavior. These nuclei send input back to the tectum, thereby providing rapid feedback to refine future output (Kinoshita et al. 2006; Meek 1983; Nevin et al. 2010; Sato et al. 2007).

In sum, the extrinsic reciprocal neuronal connections and the intrinsic neuroanatomy of the teleost tectum are complex enough to support the reentrant computational processes proposed to underlie sentience in mammals (Crick and Koch 2003; G. Edelman 1989; G.
Edelman et al. 2011; Seth et al. 2005). In mammals, neural and behavioral markers of such computational processes are associated with the neocortex and its connections to the thalamus. If the conclusion reached above is correct, then it should be possible to find similar markers associated with the tectum of fishes. Here I will provide a specific example.

2.2 Selective Attention and Tectal Neurophysiology

Feinberg and Mallat (2016) include “mechanisms for selective attention to stimuli” as one of their criteria for sensory consciousness, the process that I am calling sentience. Selective attention may be a legitimate criterion for the presence of sentience, but researchers in this area do not agree as to how this may be. Sentience and selective attention are generally not considered to be the same process, and evidence indicates that either can be present without the other (Baars 1997; van Boxtel et al. 2010; Howe et al. 2009; Tononi and Koch 2015). However, it seems undeniable that the two are related. I suggest that some form of sentient pre-attentional awareness of the world exists as long as an adequate level of arousal and general, nonspecific awareness of the environment are present. However, in the absence of selective attention, the contents of sentience required to produce specific actions necessary for survival, such as finding food or avoiding a predator, are absent. On this view, then, selective attention varies the force and focus of sentience. The implication is that, if sentience did not exist, then the processes of selective attention would have no work to do. Therefore, they would not exist. But it is indisputable that they do. Thus, agreeing with Feinberg and Mallatt, I argue that selective attention is a legitimate criterion for the presence of sentience.

A principal function of selective attention in the visual modality is to guide visual search for salient environmental items, whether these items are places of safety, a predator or food. In primates, visual search for salient environmental targets is conducted in either a parallel or serial mode (Itti and Koch 2001). The parallel mode guides attentional processes when the target object is distinct from surrounding distractor objects. Reaction time for detecting the target is very short in the parallel mode and is not lengthened by increasing the number of distractor objects. In this mode, the target is said to “pop-out” from the background distractors. Attentional processes are guided by the serial mode when the distractor items are similar to the target item. Increasing the number of distractors increases reaction time and no pop-out occurs. In primates, neocortical areas are associated with these search modes and consequent action selection (Bichot and Schall 2002; Li 2016).

Ben-Tov et al. (2015) have demonstrated both parallel and serial visual search modes in the archer fish and have found neural correlates of these processes in the optic tectum. Archer fish are able to prey on insects by hitting them with water forced from their specialized mouths. The insect is the salient object and the fish executes a visual search to locate it. Ben-Tov et al. used small rectangular bars as targets and established that the reaction time for archer fish to shoot a bar moving either faster than, or in the opposite direction from, distractor bars did not change as the number of distractors increased from 4 to 8. That is, the fish demonstrated the pop-out effect characteristic of the parallel mode of visual search. When the size of the bar was salient, reaction times for target selection increased as the number of distractors increased, indicating that the serial mode was being used.
Ben-Tov et al. identified neural correlates of pop-out in the tectum of archer fish. Discharge rates of tectal neurons correlated with characteristics of the selected target. “Speed-contrast” neurons fired at higher than baseline rates only when the speed of the target was salient while “direction-contrast” neurons fired at higher rates only when the target direction was salient. They also found “both-contrast” neurons that increased their discharge rates under either saliency condition.

Ben-Tov et al. also conducted an experiment in which the target was defined by a combination of speed and direction. Compared to selection rates for a single target feature, a target differentiated by both features was significantly more likely the be selected. When neurophysiological responses were investigated, Ben-Tov et al. found that some of the neurons that increased their firing rate to a single target increased the rate significantly more in the presence of the additive target.

In sum, archer fishes use the same attentional modes used by primates to construct a neural map of salient stimuli from a pre-attentional isomorphic neural map of the visual world. Both the isomorphic and salient neural structures are located in the tectum. The maps are dynamic and include neuronal circuits capable of associating two distinct characteristics of a visual stimulus (speed and direction of movement) to effectively drive a behavioral response. This capability may be interpreted as representing a simple form of sensory binding.

2.3 Summary

Several criteria have been suggested for a brain structure to qualify as a substrate of sentience (e.g., Crick and Koch 1990; 2003; G. Edelman 1989; Feinberg and Mallatt 2016; Seth et al. 2005). Each of these is a criterion for sentience, not sentience itself. One criterion is complexity of neural architecture and connectivity. The tectum meets this criterion. Two other criteria are isomorphic representation of sensory input and segregation of the sensory modalities. Isomorphic sensory maps are produced in the tectum. Additionally, the neural representation of each sensory modality is segregated from the others within the tectum. Another criterion is the presence of neural mechanisms for selective attention. The tectum has these mechanisms. The ability to merge, or bind, sensory input into a coherent image which can be used to direct motor output is also included. The additive effects of two distinct characteristics of a visual stimulus suggest that the tectum has this capacity. From this analysis, it is reasonable to hypothesize that the tectum is at least a part of the physical substrate of sentience in fishes.

Critics of this hypothesis are likely to insist that sentience requires structures that are homologous to the mammalian neocortex and thalamus and to maintain that the tectum and its interconnections failed to meet this requirement (e.g., Key 2015, 2016a, b; Rose 2002, 2007; Rose et al. 2012). It is also likely that critics would explain the ability of archer fish to discriminate between targets and distractors as some combination of reflex behavior and implicit discrimination learning. I admit there is room for such an argument. However, an explanation of the results of an experiment by Schuster et al. (2006) requires more than invoking implicit discrimination learning.

Although moving targets are salient for archer fish, the ability to hit one reliably takes practice. Schuster et al (2006) trained archer fish to reliably hit a target 60 cm above the water traveling at 60 mm/s. As with the experiment by Ben-Tov et al. (2015), these results
can be explained in behavioristic terms. However, the results of the second part of the experiment by Schuster et al. does not admit of such a simple explanation. They found that a second group of fishes, who only observed another fish hitting a moving target, were able to hit the target with a high rate of accuracy on their first opportunity to do so. It is difficult to explain this observation without reference to the ability of the observers to form and store in memory a mental image of other fish successfully executing the task. This is an example of declarative memory, which requires conscious awareness (Cohen et al. 1997; Eichenbaum and Cohen 2014; Squire et al. 2015), and is, therefore, a marker for the presence of sentience.

The proposal that declarative memory is necessary for the ability of archer fish to learn from observation leads to my second thesis that the pallium is a necessary component of the neural substrate for sentience in fishes. In this I diverge somewhat from the theory proposed by Feinberg and Mallatt (2016). Those authors do include a role in memory processing for the pallium in their model but they do not grant the pallium any place in the generation of mental images. Rather, the pallium simply modulates motor commands issued by the tectum (Feinberg and Mallatt 2016, Kindle edition, location 2580). I argue below that the pallium has a more central role in the formation of mental images — and, hence, in sentience in fishes — than simple modulation of tectal processing.

3. SENTIENCE IN FISHES: PALLIAL ANATOMY

3.1 Overview of Sensory-Specific Connections

The teleost pallium receives a variety of modality-specific sensory inputs (Giassi et al. 2012b; Ito and Yamamoto 2009; Northcutt 2006; Yamamoto and Ito 2008). As in mammals, all sensory modalities in fishes, other than olfaction, reach the pallium through a subpallial relay. Unlike mammals, the primary sensory relay is not the thalamus. The thalamus does contribute input to the teleost pallium (Echteler and Saidel 1981; Ito et al. 1986), but the diencephalic pregglomerular complex (PgC; Figure 1B) — a component of what Mueller (2012) named the “wider thalamus” — is the principal source of its monosynaptic sensory input (Demski 2013; Giassi et al. 2012b; Mueller 2012; Northcutt 2006; Yamamoto and Ito 2008). The PgC receives topographically organized input from the tectum (Giassi et al. 2011; Giassi et al. 2012b, c; Ito et al. 1986; Murakami et al. 1983). Therefore, the large neurons in the DC can affect motor programs or modulate sensory input to other pallial divisions.
divisions through its connections to the diencephalic and midbrain motor and sensory processing sites.

3.2 Non-Specific, Modulatory Pallial Inputs

In addition to the qualities associated with sensory input from the environment, sentience includes subjective feelings associated with motivational and affective states such as hunger, thirst and fear. These states are supported not by sensory-specific input from subcortical structures, but by subcortical input that terminates throughout the cortex (Purvis et al. 2011). In mammals, these systems are associated with the cholinergic, dopaminergic, GABAergic, serotonergic, and noradrenergic neurotransmitter systems. The same neurotransmitter systems are found in fishes (Echteler and Saidel 1981; Giassi et al. 2012b, c; Giraldez-Perez et al. 2013; Mueller and Guo 2009; Murakami et al. 1983; Schweitzer et al. 2012). The presence of dopaminergic and serotonergic input suggests that motivational and affectual systems found in mammals also exist in fishes. These neurotransmitters are involved in guiding approach and avoidance behaviors (e.g., Dayan 2012). Feinberg and Mallatt (2016) rightly include the feeling states associated with these behaviors in what they call sensory consciousness and what I am calling sentience. The existence of these neurotransmitter systems in fishes provides additional support for sentience in teleosts.

Additionally, cholinergic, noradrenergic and serotonergic afferents to the cortex affect memory, attentional processes, and states of consciousness (e.g., awake or asleep, dream sleep or non-dream sleep) in mammals (Richerson et al. 2012). The presence of widespread input containing these neurotransmitters from subpallial structures, particularly the midbrain and hypothalamus, to the pallium suggests the existence of common modulatory mechanisms for these functions in fishes and mammals.

3.3 Excitatory and Inhibitory Connections of the Pallial Divisions

Research from Leonard Maler’s laboratory at the University of Ottawa (Elliot et al., 2017; Giassi et al. 2012a, b, c; Trinh et al. 2015) exploring the pallium of two species of weakly electric knifefish has confirmed the gross pattern of intrapallial connections observed in other teleost species (Echteler and Saidel 1981; Ito and Yamamoto 2009; Northcutt, 2006), and has added important details. Excitatory neurons are required for positive feedforward and feedback control of local circuits. Inhibitory neurons are necessary for temporal stabilization and spatial sharpening of activity within these circuits.

Using immunocytochemical markers and localized injections of neurotracers, Giassi et al. (2012b, c) described the circuitry created by excitatory glutaminergic neurons. The DL has reciprocal excitatory connections to the DD, thus permitting feedforward/feedback excitation between the DL and DD. The DC receives excitatory glutaminergic input from the DL. Similar to what has been found in other species, the knifefish DC is the principal source of excitatory pallial output to diencephalic, midbrain and hindbrain targets, each of which returns excitatory input to the DL. These three regions of the fish pallium therefore have circuits that can support reentrant processing, one of the proposed requirements for a neurobiological substrate of sentience (e.g., Crick and Koch 2003; G. Edelman 1989; G. Edelman et al. 2011).
Mueller and Guo (2009) observed presumptive inhibitory GABAergic neurons in the DL, DD, DM and DC in zebrafish. Giassi et al. (2012a, c) confirmed this observation in knifefish. Giassi et al. (2012c) also observed rich intrinsic GABAergic plexuses and numerous GABAergic terminals, particularly in the DL. The source of some of this GABAergic innervation is the telencephalic subpallium (Elliot et al. 2017; Giassi et al. 2012c; VT in Figure 1B) which, in turn, receives excitatory glutaminergic input from the DM (Gaissi et al. 2012b, c). Whether the source is intrinsic or extrinsic, GABAergic terminals within the DL, DM and DD modulate the activity of excitatory glutaminergic neurons (R. Vargas et al. 2012).

3.4 Pallial Layers and Cryptic Columns in the DL

Giassi et al. (2012c) investigated the extrinsic connections of the DL and the other pallial divisions of the knifefish. In order to study the intrinsic connections of the DL, Trinh et al. (2015) incubated slices of the pallia from knifefish in nutritive media. They located the DL in the slice and used a microscope to guide injections of axonal tracers into discrete parts of it. Analysis of the resulting data indicated that the trajectory of the intrinsic axons arising from some of the large neurons within the DL separate it into ~60-µm-thick lamina along its horizontal axis. Axons from other large neurons have projections extending ~100 to 150 µm. These projections delineate columns along the vertical axis. Each column connects reciprocally to adjacent columns creating local recurrent networks throughout the DL. Thus, the DL of the knifefish pallium exhibits both a layered and a columnar organization.

Such a neuronal organization is characteristic of the mammalian cortex, but Trinh et al. (2015) emphasize that the columns observed in knifefish are not structurally discrete in the same way as columns in regions of the mammalian neocortex, such as the somatosensory cortex. Rather, they resemble the overlapping cryptic ocular dominance columns found in the visual cortex (e.g., Kaskan et al. 2007). Cryptic columnar organization allows small changes in input to one column to cause a slight shift in neuronal activity in overlapping columns, thereby allowing spatiotemporal integration of sensory input and binding.

3.5 Fish Pallial Anatomy: Summary

The research reviewed above indicates that the fish pallium has reciprocal connections with subcortical structures that provide it with both specific sensory and non-specific modulatory input. The specific sensory input to the pallium arises primarily from the PgC and is analogous to the reentrant network between the thalamus and cortex in mammals which has been proposed to correlate with conscious experience of environmental stimuli. The non-specific input comes from ventral telencephalic, diencephalic and brainstem nuclei, and contains neurotransmitters associated with affective and motivational states in mammals. My conclusion is that the teleost pallium has the neuroanatomical complexity necessary to contribute to sentience. In the next section, I will give evidence that the pallium also exhibits neurophysiological markers of sentience.
4. SENTIENCE IN FISHES: PALLIAL NEUROPHYSIOLOGY

4.1 Pallial Rhythmic Electrical Activity

There are few relevant neurophysiological experiments, and they were not specifically designed to evaluate the pallium for correlates of sentience. However, their results suggest the fish pallium exhibits generalized electrophysiological responses correlated with several criteria of sentience in mammals. For example, recordings of the electroencephalograms from the skulls of Atlantic salmon (E. Lambooji et al., 2010), African catfish (E. Lambooji et al. 2006) and the turbot (B. Lambooji et al. 2015) demonstrated that the pallium of the fish generates electrical activity in the delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–14 Hz), beta (14–30 Hz) and gamma (30 Hz and higher) bandwidths. The same spectrum of EEG frequencies is generated by the mammalian cortex and correlates with levels of arousal and, at the gamma frequency, with attentional processes and possibly with sensory binding. (Baars et al. 2013; Crick and Koch 1990; 2003; Edelman 2003; Orpwood 2013; Tononi and Edelman 1998). In addition to generalized electrophysiological responses similar to those found in the mammalian cortex, the teleost pallium shows modality-specific, sense-evoked responses (Prechtl et al. 2008; Elliot and Maier 2015).

4.2 Sensory-Evoked Activity

Prechtl et al. (1998) recorded evoked action potentials from the pallial neurons of weakly electric elephant nose fish in response to auditory, visual, mechanical (water movement), lateral line and electrical field stimulation. The electrical field stimulation was not noxious, but intended to mimic stimulation produced by the fish itself, or by conspecifics. In accord with the anatomical data described above, responses to visual stimuli were observed predominantly in the lateral pallium. Responses to electrical stimuli also occurred more laterally in the pallium, but were clustered toward its posterior (toward the tail) pole. Mechanical-stimuli-evoked responses mostly from neurons located ventromedial to the area where responses to electrical stimuli predominated and auditory-evoked responses were predominantly found in the anterior medial pallium. It is interesting that Prechtl et al. also observed that the sensory stimuli used in their study produced field potentials that oscillated in bandwidths from 15 to 55 Hz. The higher end of these bandwidths corresponds to the gamma frequency proposed, as noted previously, to be the neurobiological signature of attentional processes and sensory binding.

I indicated above that the primary interconnectivity of the DD is with other pallial divisions. Using electric brown ghost knifefish, Elliot and Maler (2015) made extracellular and patch-clamp recordings from DD neurons in response to electrosensory or acoustic stimulation. Extracellular recording revealed that DD neurons exhibited sustained discharge to electrosensory stimulation. It is interesting that the onset latency for DD neurons to respond to electrosensory stimulation was substantially longer than that found for medial pallial neurons to respond in the study by Prechtl et al. (1998). This finding is compatible with the anatomical data that indicate the DD does not receive significant direct sensory input, but adds further processing to sensory input to the DL and DM. Patch-clamp recordings indicated that the membrane potential for DD neurons went from the persistent “down” state of approximately -70 mV to an “up” state of approximately -45 mV in response to
electrosensory stimulation. The shift to a smaller negative membrane voltage indicates an increase in neuronal excitability, and these responses correlated with the frequency of extracellular spiking. Acoustic stimulation produced similar effects. In interpreting these results, Elliot and Maler (2015) hypothesized that “Up states are induced by complex and variable pallial network activity that intervenes between sensory input and DD cells” (p. 2075). The results of this experiment suggest that the DD may be involved in longer-term cognitive processing of input to other pallial divisions and can be taken as support for the proposal that the DD serves as an association region, thereby expanding the regional complexity of the pallium.

4.3 Fish Pallial Neurophysiology: Summary

Neurophysiological studies show that neurons in the fish pallium generate the same spectrum of EEG frequencies and waveforms observed in mammals. Pallial neurons also respond to sensory stimulation with specific evoked responses that show some segregation by sensory modality. Sensory stimulation also evokes EEG activity in the gamma bandwidth, a presumed correlate of attentional processes and sensory binding. Additionally, electrophysiological data support the hypothesis, generated from anatomical data, that a part of the pallium, the DD, possibly serves an associative function. These electrophysiological data are consistent with the hypothesis that the fish pallium contributes to the production of sentience in fishes.

5. THE PALLIUM AND BEHAVIORAL MARKERS OF SENTIENCE

The purpose of this section is to discuss experiments that link behavior of fishes to both the pallium and sentience. I will not discuss the substantial body of behavioral research that is supportive of my thesis that fishes are sentient because most of it was not designed to evaluate the role of the pallium in behavior. Additionally, much of it has been reviewed in recent publications (Allen 2013; Balcombe 2016; Braithwaite 2010; Brown 2014, 2016; Brown et al. 2011; Sneddon 2015).

Two general categories of behavior have dominated the published literature concerned with the behavioral functions of the fish pallium. The reason for this dominance stems from the anatomical, developmental, and molecular research that points to the medial pallium (DM – DMd and DMv in Figure 1B) of fishes as a homolog to the mammalian amygdala, and to the lateral pallium (DL – DLd/DLv) as a homolog to the mammalian hippocampus (Ganz et al. 2015; Harvey-Girard et al. 2012; Nieuwenhuys and Meek 1990; Northcutt 2006). These homologies led to the hypothesis that lesions of the DM or DL would have the same behavioral effects as lesions of the amygdala or hippocampus in mammals. Research generated primarily by researchers at the Universidad de Sevilla has largely supported this hypothesis (Portovella et al 2004a, b; Vargas et al. 2006; 2012).

5.1 Avoidance Behavior and the Pallium

As indicated earlier, I follow Allen and Trestman (2016) and define sentience broadly as the ability to have any subjective experience. This definition differs from that of Feinberg and Mallatt (2016) who regard sentience as the affective component of sensory
consciousness. Despite this definitional disagreement, I agree with their requirement that “for an animal to be ‘sentient’ it must be capable of experiencing an affective state” (Feinberg and Mallatt 2016, Kindle location 3055).

Lesions of the DM impair learned behaviors motivated by aversive stimuli in the same way that destruction of the amygdala does in mammals (Davis 1992). For example, Portavella et al. (2004a, b) assessed the effects of either DM or DL lesions on the ability of goldfish to learn a shuttle-box avoidance task. A shuttle box has two compartments. The fish had to learn to swim from one box to the other in response to presentation of a colored light (the conditioned stimulus, CS) in order to avoid electrical shock (the unconditioned stimulus, US). Portavella et al. found that DM lesions had no effect on escape from electrical shock, but significantly impaired learning of the avoidance response to the CS. DL lesions had no effect.

These results support the hypotheses that integrity of the DM is necessary for successful performance of a learned, aversively-motivated behavior and that it is a homolog of the amygdala. However, whether sentence is required to explain the acquisition of shuttle-box avoidance can be questioned. The answer to this question depends on interpretation of the two-process theory usually used to explain shuttle-box avoidance learning (Mowrer 1960). The first process is classical conditioning. The CS produces a conditioned emotional response after repeated association with the innate aversive emotional response produced by the US. The second process is operant conditioning. On one interpretation, the innate and conditioned emotional responses are equated to experience of fear. Reinforcement occurs when the avoidance response reduces fear (Mowrer 1960). Several publications describing a variety of other procedures to assess avoidance behavior in intact members of several species of fish support this view (e.g., Braithwaite 2010; Braithwaite and Boulcott 2007). If fear is considered to be a consciously experienced state, then the ability of fishes to learn shuttle-box avoidance supports the hypothesis that they are sentient. Under this interpretation, the DM is part of a distributed neural system that generates the feeling of fear. Subpallial structures comprise the core of this system, and, in conjunction with the DM, participate in elaboration of the negative affectual component of sentience in fishes.

5.2 Declarative Memory and the Pallium

Declarative memory in humans and other mammals is associated with availability for conscious recollection and provides flexible guidance to behavior in different contexts. Behaviors that require relational learning among stimuli distributed either over time or in space are considered to be exemplars of declarative memory. Transitive inference (TI) provides an excellent example (Cohen et al. 1997; Eichenbaum and Cohen 2014). TI is the ability to infer a relationship between items that have not been previously directly compared. First observing that A<B, B<C, and C<D, and then deducing that A<D is an example of TI. In humans TI requires conscious awareness of the relationships (Smith and Squire 2005). Thus, the presence of TI in a non-human species can be taken as an indication that the species is sentient.

Grosenick et al. (2007) demonstrated that male cichlid fish (Astatotiliapia burtoni) exhibit TI in an observational learning situation. Male A. burtoni inevitably fight for territory. A bystander male (BM) was placed in the center of an arena surrounded by five small compartments (A through E) with transparent walls. Each compartment housed a combatant fish (CF). CF B was introduced into CF A’s compartment, then CF C into CF B’s, and so on. Each
invader lost the ensuing fight. For example, CF A beat CF B and CF D beat CF E. CF A and CF E were then placed in separate transparent chambers and the time the BM spent near each fish was recorded. This was repeated for CF B and CF D. Although CF A had not fought with CF E, nor CF B with CF D, the BMs consistently spent more time in the vicinity of the losers (B and E) than they did in the vicinity of winners. This is a clear indication of TI and supports the hypothesis that fish are sentient.

Destruction of the hippocampus significantly impairs behaviors associated with declarative memory (Eichenbaum and Cohen 2014; Squire et al. 2015) including TI (Smith and Squire 2005). Because the DL of fishes is considered to be the homolog of the hippocampus, lesions of the DL should disrupt behaviors associated with declarative memory in fishes. The effects of DL lesions on TI in fishes have not been demonstrated, although it is a testable hypothesis that DL lesions would impair TI in archer fishes. However, other behaviors requiring relational learning have been identified in fishes (Gerlai 2017), and the effect of DL lesions on some of these has been demonstrated.

Declarative memory is distinguished from procedural or implicit memory which is unconscious and is characterized by inflexible stimulus response associations. Classical conditioning is regarded as a characteristic example of procedural memory. It is dependent upon the integrity of the cerebellum regardless of the temporal relationship between the CS and the US (Christian and Thompson 2003). The hippocampus is not required for procedural memory, including classical conditioning, except under a specific experimental design known as “trace” conditioning. In the trace procedure, the US is turned on at some time after the CS has been turned off. Thus, the term “trace” refers to the assumption that there must be some trace of the CS remaining to relate it to the US across the temporal gap between the offset of the CS and the onset of the US. This procedure differs from the “delay” procedure in which the US comes on while the CS is still present. Hippocampal destruction in humans and other mammals has no effect on conditioning in the delay procedure (Christian and Thompson 2003). Nor does destruction of the DL in the goldfish impair classical conditioning when the delay procedure is used (Gómez et al. 2016; Rodríguez-Expósito et al. 2017).

However, hippocampal destruction does impair acquisition of classical conditioning when the trace procedure is employed in both mammals (Weiss et al. 2015) and goldfish (Gómez et al. 2016; Rodríguez-Expósito 2017). These results do not mean that the cerebellum is not important in trace conditioning, as cerebellar destruction impairs trace conditioning in both mammals and fish. They are, however, interpreted to indicate that the hippocampus (or DL in fishes) functions in concert with the cerebellum in trace conditioning to enable declarative memory — and thus conscious awareness — to form a conscious image from memory to relate the CS and US across the temporal gap.

The same effect has been reported for shuttle-box avoidance learning by Portavella et al. (2004a). As described above, while DM lesions impaired shuttle-box avoidance learning, DL lesions had no effect when the delay procedure was used. However, when a trace procedure in which there was a five-second delay between the offset of the CS in the onset of the US was used, both DM and DL lesions impaired shuttle-box avoidance learning. These results are compatible with research in humans indicating that trace conditioning involves conscious awareness (Clark and Squire 1998) and hence give some support to the hypothesis that fish are sentient.

In addition to TI, Eichenbaum (2000) considers allocentric spatial learning to be a clear indication of the presence of declarative memory in animals. Allocentric spatial learning...
refers to the ability of a person or animal to encode and organize the memory system for spatial information based on the physical relationships of objects as part of a distant scene independent of the subject’s position relative to those objects. A large number of teleost species demonstrate allocentric spatial learning (e.g., Brown 2014; Durán et al. 2010; Creson et al. 2003; White and Brown 2015). The mammalian hippocampus is associated with allocentric spatial processing (Nadel 1991). The following evidence indicates that the DL is associated with spatial learning in fish.

Hippocampal neurons in rats show place-related increases in the firing rate, and hippocampal lesions impair allocentric spatial learning in rats (Nadel 1991). DL neurons in freely swimming goldfish and cichlid fish show place-related increases in the firing rate (Canfield and Mizumori 2004), and Uceda et al. (2015) observed spatial-learning-related increases in metabolic activity in the goldfish ventral DLv. Furthermore, a series of experiments from the Seville group indicate that lesions of the entire DL (e.g., Durán et al. 2010; J. Vargas et al. 2006), or just to the DLv (Bingman et al. 2017), impair allocentric spatial learning in goldfish. DM lesions, on the other hand, have no effect on allocentric spatial learning (Durán et al. 2010; J. Vargas et al. 2006).

5.3 The Pallium and Behavior: Summary

In this section I have described the results of experiments which indicate a double dissociation between the behavioral effects of DM and DL lesions. DL lesions impair behavior only when the task demands that a relationship among stimuli be maintained across time or in space. I argue that this implicates the DL in declarative memory which by general consensus implies conscious awareness. DM lesions, on the other hand, impair behaviors generally associated with procedural memory which does not require conscious awareness. However, even here, the DM may be involved in the affective component of sentience if the two-process theory of shuttle-box learning is interpreted to involve a subjective sense of fear. Particularly for the DM, the function of these pallial structures in the modulation of behavior is part of a network that includes core subpallial structures. However, I argue that the DL plays an important role in the generation of mental images, and thereby sentience, when declarative memory is required for successful execution of motor programs that are organized in brainstem structures.

6. CONCLUSION

In this target article, I have argued that fish are sentient. As indicated above, this argument has been cogently made by others based on the complexity of brainstem circuitry (e.g., Feinberg and Mallatt 2013, 2016; Merker 2007), and the flexibility and complexity of the behavior of fishes (e.g., Balcombe 2016; Braithwaite 2010; Brown 2014; Brown et al. 2011). I have also argued that the intrinsic neuroanatomical organization and extrinsic connections of the pallium, particularly with the PgC and the tectum, are complex enough to be at least weakly analogous to the circuitry of the cortex and thalamus assumed by some to underlie sentience in mammals. Neurophysiological and behavioral data further support the hypothesis that fish have the capacity for sentience.

Based on the evidence reviewed in this paper, I suggest that the pallium is an important part of the hierarchical network proposed by Feinberg and Mallatt (2016) to
underlie sentience in fishes. The tectum is at the core of this network. The tectum receives segregated sensory input and has the local and global reentrant neural circuitry needed to amplify and process this input. Segregation of the sensory modalities is maintained through the PgC to the pallium. The pallium also receives input from subpallial structures involved in placing a positive or negative valence on this input. These inputs are then integrated by various divisions of the pallium. Particularly in the case of the DL and declarative memory, the result of this integration is the formation of mental images that permit relational interactions among stimuli and flexible regulation of behaviors organized in the brainstem.

In her book Animal Minds, Andrews (2015) makes the point that, “Members of the human species have human minds, and if members of other species have minds, they will have species-specific minds of their own” (p. 4). It is safe to say the same about those processes of the mind of fishes I call sentience. Fish sentience differs from human sentience, and what it feels like is as unknowable to us as what it feels like to be a bat. However, just as Nagel (1974) found it reasonable for there to be something it feels like to be a bat, I think that it is reasonable to adduce from the existing evidence that there is something it feels like to be a fish.

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The Other Minds Problem: Animal Sentience and Cognition

Overview. Since Descartes, philosophers know there is no way to know for sure what — or whether — others feel (not even if they tell you). Science, however, is not about certainty but about probability and evidence. The 7.5 billion individual members of the human species can tell us what they are feeling. But there are 9 million other species on the planet (20 quintillion individuals), from elephants to jellyfish, with which humans share biological and cognitive ancestry, but not one other species can speak: Which of them can feel — and what do they feel? Their human spokespersons — the comparative psychologists, ethologists, evolutionists, and cognitive neurobiologists who are the world’s leading experts in “mind-reading” other species -- will provide a sweeping panorama of what it feels like to be an elephant, ape, whale, cow, pig, dog, bat, chicken, fish, lizard, lobster, snail: This growing body of facts about nonhuman sentience has profound implications not only for our understanding of human cognition, but for our treatment of other sentient species.

| Gregory Berns: Decoding the Dog's Mind with Awake Neuroimaging |
| Gordon Burghardt: Probing the Umwelt of Reptiles |
| Jon Sakata: Audience Effects on Communication Signals |
| PANEL 1: Reptiles, Birds and Mammals |
| WORKSHOP 1: Kristin Andrews: The “Other” Problems: Mind, Behavior, and Agency |
| Sarah Brosnan: How Do Primates Feel About Their Social Partners? |
| Alexander Ophir: The Cognitive Ecology of Monogamy |
| Michael Hendricks: Integrating Action and Perception in a Small Nervous System |
| PANEL 2: Primates, Voles and Worms |
| WORKSHOP 2: Jonathan Birch: Animal Sentence and the Precautionary Principle |
| Malcolm Maclver: How Sentence Changed After Fish Invaded Land 385 Million Years Ago |
| Sarah Woolley: Neural Mechanisms of Preference in Female Songbird |
| Simon Reader: Animal Social Learning: Implications for Understanding Others |
| PANEL 3: Sea to Land to Air |
| WORKSHOP 3: Steven M. Wise: Nonhuman Personhood |
| Tomoko Ohyama: Action Selection in a Small Brain (Drosophila Maggot) |
| Mike Ryan: "Crazy Love": Nonlinearity and Irrationality in Mate Choice |
| Louis Lefebvre: Animal Innovation: From Ecology to Neurotransmitters |
| PANEL 4: Maggots, Frogs and Birds: Flexibility Evolving |
| SPECIAL EVENT: Mario Cyr: Polar Bears |
| Collin Chapman: Why Do We Want to Think People Are Different? |
| Vladimir Pradosudov: Chickadee Spatial Cognition |
| Jonathan Balcombe: The Sentient World of Fishes |
| PANEL 5: Like-Mindedness and Unlike-Mindedness |
| WORKSHOP 5 (part 1): Gary Comstock: A Cow's Concept of Her Future |
| WORKSHOP 5 (part 2): Jean-Jacques Kona-Boun: Physical and Mental Risks to Cattle and Horses in Rodeos |
| Joshua Plotnik: Thoughtful Trunks: Application of Elephant Cognition for Elephant Conservation |
| Lori Marino: Who Are Dolphins? |
| PANEL 6: Mammals All, Great and Small |
| Larry Young: The Neurobiology of Social Bonding, Empathy and Social Loss in Monogamous Voles |
| WORKSHOP 6: Lori Marino: The Inconvenient Truth About Thinking Chickens |
| Andrew Adamatzky: Slime Mould: Cognition Through Computation |
| Frantisek Baluska & Stefano Mancuso: What a Plant Knows and Perceives |
| Arthur Reber: A Novel Theory of the Origin of Mind: Conversations With a Caterpillar and a Bacterium |
| PANEL 7: Microbes, Molds and Plants |
| WORKSHOP 7: Suzanne Held & Michael Mendl: Pig Cognition and Why It Matters |
| James Simmons: What Is It Like To Be A Bat? |
| Debbie Kelly: Spatial Cognition in Food-Storing Steves |
| Steve Phelps: Social Cognition Across Species |
| PANEL 8: Social Space |
| WORKSHOP 8: To be announced |
| Lars Chittka: The Mind of the Bee |
| Reuven Dukas: Insect Emotions: Mechanisms and Evolutionary Biology |
| Adam Shriver: Do Human Lesion Studies Tell Us the Cortex is Required for Pain Experiences? |
| PANEL 9: The Invertebrate Mind |
| WORKSHOP 9: Delcianna Winders: Nonhuman Animals in Sport and Entertainment |
| Carel ten Cate: Avian Capacity for Categorization and Abstraction |
| Jennifer Mather: Do Squid Have a Sense of Self? |
| Steve Chang: Neurobiology of Monkeys Thinking About Other Monkeys |
| PANEL 10: Others in Mind |
| WORKSHOP 10: The Legal Status of Sentient Nonhuman Species |