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Title:
Perceptual rivalry across animal species

Date:
2020-12-01

Citation:
Carter, O., van Swinderen, B., Leopold, D. A., Collin, S. P. & Maier, A. (2020). Perceptual rivalry across animal species. Journal of Comparative Neurology, 528 (17), pp.3123-3133. https://doi.org/10.1002/cne.24939.

Persistent Link:
https://hdl.handle.net/11343/275799

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Perceptual rivalry across animal species

(for the special issue honouring Jack Pettigrew)

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Running Title: Perceptual rivalry across animal species

Key Words: Binocular Rivalry, Multistable, Perception, Suppression, Primate, Drosophila, Fish

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/cne.24939

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Abstract

This review in memoriam of Jack Pettigrew provides an overview of past and current research into the phenomenon of multistable perception across multiple animal species. Multistable perception is characterized by two or more perceptual interpretations spontaneously alternating, or rivalling, when animals are exposed to stimuli with inherent sensory ambiguity. There is a wide array of ambiguous stimuli across sensory modalities, ranging from the configural changes observed in simple line drawings, such as the famous Necker cube, to the alternating perception of entire visual scenes that can be instigated by interocular conflict. The latter phenomenon, called binocular rivalry, in particular caught the attention of the late Jack Pettigrew, who combined his interest in the neuronal basis of perception with a unique comparative biological approach that considered ambiguous sensation as a fundamental problem of sensory systems that has shaped the brain throughout evolution. Here, we examine the research findings on visual perceptual alternation and suppression in a wide variety of species including insects, fish, reptiles and primates. We highlight several interesting commonalities across species and behavioral indicators of perceptual alternation. In addition, we show how the comparative approach provides new avenues for understanding how the brain suppresses opposing sensory signals and generates alternations in perceptual dominance.

Contents

1. Introduction.....**3**

2. Behavioural evidence of perceptual rivalry across animal species.....**5**

2.1. Insects **5**

2.2. Fish and Reptiles..... **7**

2.3. Primates.....**7**

3. Understanding perceptual suppression through rivalry.....**8**

3.1. Insects.....**8**

3.2. Primates.....**9**

4. **Identifying the processes that underly perceptual switching** **11**

4.1. Insects.....**11**

4.2. Fish and Reptiles.....**13**

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4.3. Primates.....13
5. When the switching stops.....14
6. Conclusion.....15

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1. Introduction

As we navigate our visual environment, we are continuously bombarded with new sensory information that can be simultaneously ambiguous, incomplete and overabundant. While it remains unclear exactly how the brains of humans and other animals deal with the fundamental problem of structuring the sensory input, much has been learnt over the last 50 years – including insights that have drawn upon comparative approaches.

Inspired by the life and extraordinary breadth of research pioneered by the late Jack Pettigrew, this review will focus on perceptual rivalry, or multistable perception, and the lessons learnt by looking at brain responses to ambiguous sensory stimuli across a range of animal species. "Perceptual rivalry" refers to the perceptual alternations that typically result from the presentation of conflicting or ambiguous sensory inputs that can be validly interpreted in more than one way. Well known examples include Necker's cube (Necker, 1832; Wheatstone, 1838), Duck-Rabbit and vase-face illusion (Figure 1a), which count among a limitless number of perceptually unstable stimuli that can be generated systematically.

One particularly striking example of perceptual rivalry that has dominated research in human and non-human primates is binocular rivalry. During binocular rivalry, two different stimuli that cannot be fused into a combined image, are simultaneously presented to each eye. Under these conditions, an observer typically will not experience perceptual merging of the two images, as one might guess. Instead, the observer reliably experiences a dynamic "rivalry" for awareness between the two competing monocular stimuli (Figure 1b). As only one of the two eye's stimuli dominates perception at a given time, the other stimulus is said to be

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perceptually suppressed by the brain (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006; Walker, 1975; Wheatstone, 1838). While perceptual rivalry has typically been studied in the domain of vision, the same pattern of perceptual alternations has now been demonstrated across a range of non-visual modalities including audition (Pressnitzer & Hupé, 2006; Snyder, Holder, Weintraub, Carter, & Alain, 2009), touch (Carter, Konkle, Wang, Hayward, & Moore, 2008) and olfaction (Zhou & Chen, 2009).

During sustained presentation of such stimuli, human observers typically report an unpredictable sequence of switches in perceptual dominance over time. These types of stimuli have been a major focus of research for many years because the characteristic alternations in perceptual awareness induced by these stimuli provide a controlled method for scientific investigation. In binocular rivalry, for example, researchers can parametrically design visual stimuli to investigate i) *perceptual suppression* of the retinal information and ii) *perceptual alternation* of the content from the two eyes. Human psychophysicists have explored the nature of binocular rivalry in detail and revealed a competitive process in which suppressed stimuli are unseen, but nonetheless surprisingly potent. In fact, the structure of a stimulus determines how long it will remain suppressed, after which time it abruptly rises to perceptual dominance as its competitor is rendered invisible by the brain (for review see Blake & Logothetis, 2002).

[Insert Figure 1 here]

Central to Jack Pettigrew's interest in perceptual rivalry was the idea that these periodic alternations in perceptual state and accompanying changes in brain activity must serve, or reflect, a biological purpose. For example, analogous to brain mechanisms that promote behavioural exploration, it is easy to imagine why a periodic perceptual "switch" might be important to disengage a persistent perceptual interpretation in a visual world riddled with visual ambiguity and binocular conflict. Perceptual alternations might thus serve as a central

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perceptual fail-safe mechanism to ensure that an animal does not become "stuck" in an unfavourable perceptual interpretation. A capacity that may be particularly important if the surrounding stimuli are rapidly changing. Following this logic, it seems relevant to ask which animals, from non-human primates through to reptiles, fish or even invertebrates demonstrate rivalry-like processes, as this would suggest that these perceptual alternations might be deeply linked to conserved evolutionary processes.

Below in sections 2-4 we review the scientific approaches to identifying and understanding perceptual alternations across different animal species. We begin by reviewing the behavioral evidence of perceptual rivalry-like phenomena in insects, fish, reptiles and both human and non-human primates (section 2). Following this, some of the key findings relating to perceptual suppression mechanisms that have resulted from studies using rivalry-inducing paradigms are discussed (section 3). We then explore the literature that has helped to uncover the nature of the switch and the processes driving perceptual alternations across species (section 4). Prior to concluding, we indulge in a brief digression and consider some of Jack's more unusual and memorable research contributions relating to perceptual rivalry that have focused on the unusual circumstances that can lead to a break-down of the switching process (section 5).

2. Behavioural evidence of perceptual rivalry across animal species

While it is impossible to cover the full spectrum of animal research that is relevant to rivalry, the following contributions are highlighted both because they represent key examples along different arms of the evolutionary tree that impacted Jack's thinking and represent major advances in the scientific literature.

2.1. Insects:

Insects diverged from humans and vertebrates more than 700 million years ago (Kaas, 2016). However, they share the same need to allocate limited sensory resources appropriately

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between the conflicting visual stimuli impacting two opposing eyes as all bilaterians. There is now increasing evidence that this competition is resolved through a process involving alternations in attention, meaning that stimuli can be transiently suppressed from evoking a perceptual or behavioural response. For example, early evidence showed that freely behaving hoverflies (*Syritta pipiens*) exhibit flight manoeuvres that are dependent on the visual structure of the surroundings and reminiscent of eye saccades in mammals (Collett & Land, 1975). These flight saccades appear to promote an adaptive sampling of the visual environment (Heisenberg, 1983; Land, 2019). The extent to which this saccadic activity in these small-brained animals is generative as opposed to merely reflexive has been debated (Censi, Straw, Sayaman, Murray, & Dickinson, 2013; Heisenberg, 2015). However, it is now clear that insects are the smallest bilaterians for which evidence shows the allocation of limited neural processing resources in way that allows the animals to concentrate on a discrete aspect of sensory information while ignoring other perceivable information. This includes evidence of periodic switching between what is selected and suppressed (de Bivort & van Swinderen, 2016).

Already back in the early 1980's Martin Heisenberg and Reinhard Wolf showed compelling evidence that flies switched between competing percepts. *Drosophila melanogaster* flies in tethered flight modulate their wingbeat behaviour to match the closed-loop requirements for fixating (or stabilising) visual objects (Heisenberg & Wolf, 1984), and when two visual objects (or patterns) are presented in competition they alternate between the two different behavioural programs (Heisenberg & Wolf, 1984). These original experiments were entirely mechanical, with the tethered fly's torque behaviour controlling (via negative feedback) the rotation of transparent cylinders layered around it, upon which were painted different patterns (Figure 2a).

After initial demonstrations of fly multi-stable fixation reported by (Heisenberg & Wolf, 1984), the same group has confirmed this (almost 40 years later!), now using an electronic system

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to display overlayed competing patterns (Toepfer, Wolf, & Heisenberg, 2018). The study demonstrated that these alternations in fly fixation behaviour did not depend on binocular competition; they also occurred when the competing patterns were presented to only one eye (Toepfer et al., 2018) suggesting a selective process is driving the alternations. Importantly, there was evidence of stochasticity to this process that bears similarities with multi-stable perception dynamics in humans (e.g., a gamma-distribution of alternations Levelt, 1967).

[Insert Figure 2 here]

Experiments from the same group examined this behaviour in flies, by investigating if the insect's responsiveness could be biased to a visual event on one side when two were presented simultaneously to either eye (Sareen, Wolf, & Heisenberg, 2011). In a typical experiment, flies are presented with competing objects that would normally evoke an optomotor response (registered as a torque to the left or to the right) when presented on their own. When presented together (one to either eye), responsiveness to the left or right seems random, and is evenly distributed (50:50). However, if one of the objects is cued (by for example flashing it briefly prior to the test), optomotor responses are biased towards the cued side (Sareen et al., 2011). This experimental setting allowed for incisive questions to be asked about *Drosophila* attention, and how it might relate to rivalry. For example, bias to the cued side lasted about 4 seconds, suggesting a timeframe for perceptual switching in flies (Sareen et al., 2011). When left and right stimuli were identical (non-cued), it was noted that flies tended to respond several times in a row to the same side, before switching to the other side, a phenomenon called chaining (Koenig, Wolf, & Heisenberg, 2016). This alternation between the identical stimuli presented to either eye was associated with a dwell-time or inertia that seemed endogenously controlled and could be taken as behavioural evidence that perceptual rivalry does indeed occur in the fly.

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2.2. Fish and Reptiles:

While Jack never worked with insects, he described with fascination the independence of eye-movements in the sand lance (*Limnichthyes fasciatus*, Teleostei) and chameleons (*Chamaeleo spec.,* Reptilia) (Figure 2b). In 1999, Pettigrew and Colleagues noted how the wide visual fields sampled by the independently-moving eyes and the rapid strikes at moving prey in both the sand lance and the chameleon may have selected for high levels of alternating rivalry as both a predatory and anti-predation strategy (Pettigrew et al., 1999). In both species, the eyes alternate, with a series of saccades in one eye, while the other eye is quiescent, followed by a series of saccades in the other eye. However, the eyes never make saccades (rapid eye movements) at the same time in both eyes. As these species have crossed visual pathways, this pattern of eye movements implies an interhemispheric switch process that was a central theme through much of Jack's research (described in more detail in section 4).

2.3. Primates:

In terms of non-human primates, the largest body of perceptual rivalry research has involved macaque monkeys (*Macaca spec.*), both on the behavioural as well as the neuronal level. One reason for this choice is the phylogenetic proximity of Macaques and humans (Kaas, 1992). The early visual system of macaques is remarkably similar to that of humans (Roelfsema & Treue, 2014), down to the molecular level of gene expression patterns (Bernard et al., 2012; Takahata et al., 2006). Not surprisingly then, macaque visual performance has consistently been found to be close to that of humans (Buracas & Albright, 1999; Elmore & Wright, 2015; Gelfand & Horwitz, 2018; Harwerth, 1982; Kaas, 1992; Levi, Yates, Huk, & Katz, 2018; Lynn & Curran, 2010; Rajalingham, Schmidt, & DiCarlo, 2015; Zarco, Merchant, Prado, & Mendez, 2009). Macaques have also been shown to perceive multistable visual stimuli perceptually fluctuating with a temporal profile that is similar to that of humans (Dodd, Krug, Cumming, & Parker, 2001; Grunewald, Bradley, & Andersen, 2002; Leopold & Logothetis, 1996; Leopold, Maier, & Logothetis, 2003; Leopold, Maier, Wilke, & Logothetis, 2005; Logothetis & Schall,

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1989; Myerson, Miezin, & Allman, 1981). In some cases, macaques were trained to indicate their perceptual switching, whereas in other cases researchers have relied on objective indicators, such as the alternating pattern of eye movements associated with each of the competing percepts (Figure 3, for review see Leopold et al., 2003). In addition to providing evidence that such animals are valid models to inform understandings of rivalry in humans, the temporal similarities across animal species are suggestive of an evolutionarily conserved switching mechanism.

[Insert Figure 3 here]

3. Understanding perceptual suppression through rivalry

Much has been written about the use of perceptual rivalries to investigate the neural correlates of conscious awareness and suppression (Alais & Blake, 1999, 2005; Blake & Logothetis, 2002; Crick, 1996; Leopold & Logothetis, 1996, 1999; Logothetis, 1998; Watson, Pearson, & Clifford, 2004). In the previous section, behavioural evidence for alternating perceptual dominance characterising of perceptual rivalry was discussed. This section will focus on research conducted in insects and both human and non-human primates that have contributed to our current understanding of both perceptual suppressive mechanisms and the impact of supressed sensory data on brain activity and behaviour.

3.1. Insects:

Neural correlates of perceptual rivalry have been demonstrated in insects by inserting miniature extracellular electrodes into the optic lobes of tethered flies presented with competing gratings shown to either eye, using an experimental protocol similar to that depicted in Figure 2a (Tang & Juusola, 2010). The electrodes recorded local field potentials (LFPs), which reflect an aggregate of neuronal activity, similar to an EEG (Buzsaki, 2006). As described in section 2.1., flies confronted with competing gratings presented to either eye,

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alternated between trying to fly to the left or to the right. In terms of the electrophysiological responses, these behavioural alternations were matched with alternating LFP power in the left or right optic lobes, suggesting a level of suppression for the ignored grating on the other side. Both behaviour and LFP activity alternated in correlation although not all flies alternated at the same rate, suggesting individual variability in switching.

Interestingly, behavioural switches were preceded by changes in brain activity (the ignored hemisphere gained power over time), suggesting an endogenous mechanism was driving the switches (Tang & Juusola, 2010). One simple explanation is a mechanism driving alternations in hemispheric dominance. However, a subsequent study showed that rivalry-like alternations recorded from the fly brain could also be evoked from single objects composed of competing parts, and thus did not require competition from either eye (van Swinderen, 2012). In that study, flies flying in a virtual reality arena fixated on complex shapes grouped in a centre-surround arrangement, where the centre and the surround flickered at distinct frequencies. These frequencies, detected as steady-state visually-evoked potentials (SSVEPs) in the fly brain, alternated in amplitude without the fly necessarily switching behavioural programs. Consistent with the insect behavioural work discussed in section 2 suggesting that rivalry persists when bistable images are presented to only one eye (Toepfer et al., 2018), this electrophysiological study again suggests a more fundamental, perhaps attention-like mechanism, rather than perceptual rivalry *per se*. Indeed, like attention in other animals, this type of alternations can be detected in the fly brain even without correlated behavioral programs, something that had also been shown in previous studies recording LFPs from non-flying flies (van Swinderen, 2007; van Swinderen & Brembs, 2010; van Swinderen & Greenspan, 2003). Together these studies in the smallest animal brains place a spotlight on the question of the mechanism driving these switches in perceptual dominance.

3.2. Primates

In human and non-human primate research, one variant of interocular suppression that has been particularly valuable in teasing apart the neural processes underlying the

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suppression or awareness of visual stimuli is flash suppression. In this paradigm perceptual invisibility of a stimulus presented to one eye is generated when a second, "rivalling" stimulus is flashed at either the same position as the other eye (Lansing, 1964; McDougall, 1901; Wolfe, 1984) or close to the same position (Bonneh, Cooperman, & Sagi, 2001; Kanai & Kamitani, 2003; Maier, Logothetis, & Leopold, 2005; Simons et al., 2006; Wilke, Logothetis, & Leopold, 2003). If one eye's stimulus remains constant while the other eye is subject to an ongoing stream of visual flashes, prolonged periods of perceptual suppression of the constant eye can be induced that last up to minutes (Maruya, Watanabe, & Watanabe, 2008; Tsuchiya, Koch, Gilroy, & Blake, 2006; Yang & Blake, 2012). Human observers report no conscious access to stimuli that are perceptually suppressed, yet some features of the stimuli seem to nonetheless influence behaviour. For example, it has been shown that information about the position of erotic (Jiang, Costello, Fang, Huang, & He, 2006) and otherwise emotionally arousing (such as threatening) pictures (Yamada & Kawabe, 2011) or words (Yang & Yeh, 2011) can influence behaviour, even when the stimuli remained suppressed. Similarly, visual object categorization might affect suppressed stimuli (Almeida, Mahon, Nakayama, & Caramazza, 2008) (but see: Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012). Lastly, subjects respond faster to images of objects that they previously encountered during perceptual suppression (Chou & Yeh, 2012); (but see: Schall, Nawrot, Blake, & Yu, 1993).

On a single neuron level, the effects of binocular rivalry flash suppression have been studied using microelectrode recordings in macaque monkeys (Maier, Logothetis, & Leopold, 2007; Panagiotaropoulos, Deco, Kapoor, & Logothetis, 2012; Sheinberg & Logothetis, 1997). See Leopold et al, (2003) for a review of techniques to obtain reliable perceptual data from animals. Similar findings were made in human neurosurgical patients (Kreiman, Fried, & Koch, 2002), which are more limited in scope due to the fact that epileptic foci generally reside outside occipital visual cortical areas. The work in macaques convincingly showed that the percentage of neurons that co-fluctuate in activity with perceptual alternations increases from lower sensory cortex towards higher-level visual brain areas (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). A similar trend is seen in

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human fMRI studies (Fang & He, 2005; Polonsky, Blake, Braun, & Heeger, 2000; Rees, Friston, & Koch, 2000; Tong et al., 2006; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Tse, Martinez-Conde, Schlegel, & Macknik, 2005). Interestingly human fMRI also reveal amygdala activation for perceptually suppressed faces with socially relevant emotional expressions (Amting, Greening, & Mitchell, 2010; Lerner et al., 2012; Pasley, Mayes, & Schultz, 2004; Troiani, Price, & Schultz, 2014; Williams, Morris, McGlone, Abbott, & Mattingley, 2004).

4. Identifying the processes that underly perceptual switching.

In addition to understanding the neural processes associated with the suppression vs awareness of sensory stimuli, Jack was fascinated by the apparently oscillatory nature of the perceptual switches. This interest was captured by his paper titled "*Searching for the Switch: Neural bases of perceptual rivalry alternations*" (Pettigrew, 2001) which set the stage for much of the work that followed. With typical flare, Jack highlighted the need to better understand the nature and impact of oscillatory brain activity (Pettigrew, 2001). In addition to his own deep knowledge of different animal species, he even credited the late Nobel Prize winning physicist Richard Feynman with providing some conceptual inspiration through personal conversations in the halls of Caltech (J. D. Pettigrew & Carter, 2005).

Here we review findings from the animal literature to gain a better appreciation of mechanisms driving perceptual alternations from humans down to some of the smallest brains. In the process, we attempt to uncover the bases of the perceptual switch that fascinated Jack so much and consider evidence of fundamental brain processes that exist across species.

4.1. Insects:

If there is a switch, it should be possible to find it in *Drosophila*, which gave us insight into a variety of neural switches, such as clock-like circuits controlling sleep and waking (for example see Dubowy & Sehgal, 2017). One of the advantages of working with animal models such as fruit flies is that, *Drosophila melanogaster* offers genetic tools for efficiently identifying the

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neural substrates underpinning behavioural processes such as rivalry. One of these genetic tools is calcium imaging, which provides a way of tracking the activity of specific neurons in the animal's brain as it performs various behaviors. The obvious question in terms of rivalry, is which neurons light up when flies make left versus right choices in a virtual reality arena? Two recent studies identified bilateral glomeruli (clutches of neurons) in the fly brain that appeared to be in competition when identical stimuli were presented simultaneously to either eye (Shiozaki & Kazama, 2017; Sun et al., 2017). Each glomerulus includes neurons that are activated by the ipsilateral stimulus and inhibited by the contralateral stimulus, as well as neurons in the same glomerulus that do exactly the opposite. This apparent counterbalanced equilibrium seems to be offset in part by the fly's behavioural history, with some of these neurons also responding to self-motion, and thereby breaking the balance. The bilateral glomeruli project to neurons in the fly's central brain called the 'ellipsoid body', a donut-like structure, where the interhemispheric competition is somehow resolved. The fly's sensory focus is represented as a single 'bump' of calcium activity, moving egocentrically around the ellipsoid body (Seelig & Jayaraman, 2015). Rivalry is evident by the bump switching positions to represent either competing object, but, interestingly, there is always only one bump. The single bump even persists for a while in the dark, after the visual stimuli have been turned off. This is strong evidence that even the smallest animal brains are endowed with an endogenous perceptual switch, that is driven in part by interhemispheric competition, but that like attention is also driven by other intrinsic processes such as hysteresis or memory. However, is it really a switch (i.e., a flip-flop circuit) or, rather, an emergent property of many neurons or even the whole brain?

A recent electrophysiological study in honeybees suggests that whole-brain oscillatory dynamics may be gating these apparent perceptual alternations (Popov & Szyszka, 2020). Paired LFP recordings from bilateral neuropils called mushroom bodies (MBs) revealed spontaneously generated 18Hz (high 'alpha') oscillations that biased the phase of both spikes and high frequency neural activity on each side. Like human alpha (Buzsaki, 2006), the

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oscillations were dampened by stimuli, such as odours, and cross-frequency coupling revealed an effect on information transmission and connectivity within and between the hemispheres. Thus, the timing of spikes in the right hemisphere was phase-coupled to the 18Hz oscillation in the left hemisphere. Interestingly, the flow of information was not equal between hemispheres: Granger causality analysis revealed a right-over-left dominance (Popov & Szyszka, 2020). This work in bees suggests that interhemispheric switching and lateralization may indeed be an evolutionarily ancient phenomenon in bilaterians. However, the switching mechanism may stem from a whole-brain process (e.g., alpha oscillations) rather than a specific circuit.

4.2. Fish and Reptiles:

As discussed above in section 2.2., the sand lance demonstrates clearly independent eye movements, consistent with alternating perceptual dominance, characteristic of perceptual rivalry. While other species of teleosts also possess independent eye movements (i.e. the pipefish, *Corythoichthyes intestinalis* and the weeverfish, *Parapercis cylindrica*), and, like most teleosts, have a high degree of crossed visual pathways, little or no research has been conducted into the neurophysiological processes involved in resolving of binocular conflict in fishes. Interestingly, these lateral-eyed species all possess foveae and rely on high acuity vision, which may indicate the necessity to alternate input from the two eyes when the eyes are sampling different parts of the visual field, where there may be a risk of interocular targeting rivalry. Interestingly, and unlike all other vertebrates investigated thus far (Land, 1995), the sand lance possesses large post-saccadic drifts as part of its normal oculomotor repertoire. It is unknown whether this shows that perceptual rivalry in this species alters with eye position or whether the post saccadic drifts are in some way advantageous to the sand lance and not simply a sign of an inaccurate oculomotor system (Fritsches & Marshall, 1999). Land (1999) suggests that since the background of seawater against which the sand lance targets its small, mobile prey is relatively featureless, the poor spatial detail might lead to rather loose optokinetic stabilisation, making drifting inevitable. On the other hand, the slow

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re-alignment of the two eyes to a position, which enables an increased field of view may enhance predatory surveillance and reduce the likelihood of binocular conflict. The degree of perceptual rivalry in the context of the levels of independent eye movement and oculomotor responses may also depend on the linkage (conjugacy) between the eyes in response to visual input (Fritsches & Marshall, 2002).

4.3. Primates:

In humans and other primates, considerable research has investigated the temporal dynamics of binocular rivalry, beginning with Levelt's seminal work (Levelt, 1966, 1967). A critical element of binocular rivalry is that perceptually suppressed stimuli not only penetrate the visual system but are critical for shaping the temporal alternation dynamics (for review see Brascamp, Klink, & Levelt, 2015). The neural basis of perceptual switching is poorly understood and has historically divided into different schools of thought. In one school of thought is that perceptual alternation is initiated by visual competition in retinotopically organized areas (Alais, Cass, O'Shea, & Blake, 2010; Said & Heeger, 2013; Wilson, 2003). According to this view, alternation proceeds according to reciprocal dynamics of circuits responding to the competing sensory patterns (for review see Blake & Logothetis, 2002; Tong et al., 2006). This view is supported by significant psychophysical and brain imaging evidence (Brascamp, Sohn, Lee, & Blake, 2013; Lee, Blake, & Heeger, 2007). A competing view has held that perceptual switching is less linked to the sensory circuitry and more related to active elements of perception, such as attention and even eye movements (Leopold & Logothetis, 1999). This view is also supported by brain imaging evidence (Lumer, Friston, & Rees, 1998; Lumer & Rees, 1999). Intriguing phenomena that specifically probe the alternation process, such as perceptual stabilization (Leopold, Wilke, Maier, & Logothetis, 2002) and perceptual juggling (Leopold et al., 2003) can be interpreted within either framework.

Jack's view of perceptual alternation was not clearly rooted in either of these perspectives, but rather envisioned orchestration by an external oscillator located in the brain stem that coordinated regular switches in dominance between the two cortical hemispheres

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(Pettigrew, 2001). Jack was also particularly interested in the idea that 'aberrant' rivalry dynamics may be indicative of maladaptive human conditions and that a slow interhemispheric switch may directly underlie symptoms of bipolar disorder (Miller et al., 2003; Miller et al., 2010; Pettigrew & Miller, 1998). We direct the reader to the review by Miller in the current issue that describes in detail, Jack's views on interhemispheric switching, perceptual rivalry, and bipolar disorder (Miller, in press). More recently, some further research exploring individual differences has looked at correlations between switching rate and personality traits (Antinori, Carter, & Smillie, 2017; Antinori, Smillie, & Carter, 2016; Thakkar, Antinori, Carter, & Brascamp, 2019).

5. When the switching stops

As described in detail above, perceptual rivalry is - by definition - a process involving competition between conflicting perceptual representations of available sensory data. Rivalry is characterised by switches between suppression and dominance of the competing perceptual interpretations. However, there are instances when the switching appears to stop, and an observer will experience a patchwork or combination of the rivalling percepts. The authors of this review are unaware of any research in insects, flies, reptiles or non-human primates investigating the existence or underlying mechanisms of such mixed states. Indeed, data collected during periods when the animal's perceptual state is uncertain is typically removed prior to analysis (in both human and non-human animal research).

In the spirit of the current review, motivated partly as a tribute to Jack's contribution to research, the authors felt it important to take this opportunity to highlight some of Jack's more unusual research (which is saying a lot!). First there was the series of binocular rivalry experiments and collaborations involving administration of psilocybin in Switzerland (Carter et al., 2007; Carter, Pettigrew, et al., 2005) and ayahuasca in Brazil (Frecska, White, & Luna, 2004) and the impact of meditation in Tibetan Buddhist Monks (conducted with the expressed support of HH the Dalai Lama) (Carter, Presti, et al., 2005). It is not clear why this might be the case, but a feature of both the impact of psychedelic drugs and focused

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meditation was an apparent weakening of the switch process itself with significant increases in mixed percepts reported in both cases (Carter et al., 2007; Carter, Presti, et al., 2005). Separate to this research was a sole author study published by Jack reporting that periods of laughter abolish binocular rivalry (Pettigrew, 2005). In the way only Jack could, there is an admission in the methods section that while the participants were naïve about the hypothesis "the hilarity associated with the experiment and its preparations, such as the selection of suitable jokes, were impossible to hide." After reporting the effects of laughter on rivalry alternations, the discussion included a detailed account of the possible evolutionary function of laughter (Pettigrew, 2005). This was followed by reports of a truly remarkable finding. It was noted that the effects of laughter on rivalry can also be "interrupted by the laughter-like sudden shift in motivation associated with orgasm (JD Pettigrew, unpublished observation)." The authors appreciate the novelty of this insight but are hopeful that this finding will rest with Jack, never to be replicated!

6. Conclusion

The alternating periods of suppression and dominance associated with rivalry has been the focus of a wide body of research. Here, we have attempted to summarise some of the work looking at rivalry-like alternations across a range of animal species. We considered both human and non-human primates as well as animals with oppositely facing, independently moving eyes (like chameleons, sand lances, pipefishes and many flies). We present clear evidence that the same characteristics of perceptual switching that are well described in the human literature can also be seen in a range of phylogenetically distant species. Together, this research strongly supports the idea that perceptual alternations might provide an evolutionary advantage to all brains that face ambiguous sensory inputs. We thank Jack for all of his important contributions to better understanding "the switch".

Author acknowledgements

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The work of OC was supported by an Australian Research Council Future Fellowship (FT140100807). AM is supported by a research grant from the National Eye Institute (1R01EY027402-03) and DL Intramural Research Program of the National Institute of Mental Health (ZIA MH002838).

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Figure Legends

Figure 1. a) Human observers typically report perceptual alternations when viewing the Necker's Cube, Duck-Rabbit and Face-vase illusions (from left to right). b) When two different images are simultaneously presented to each eye, one image will tend to dominate at a time while the other is suppressed.

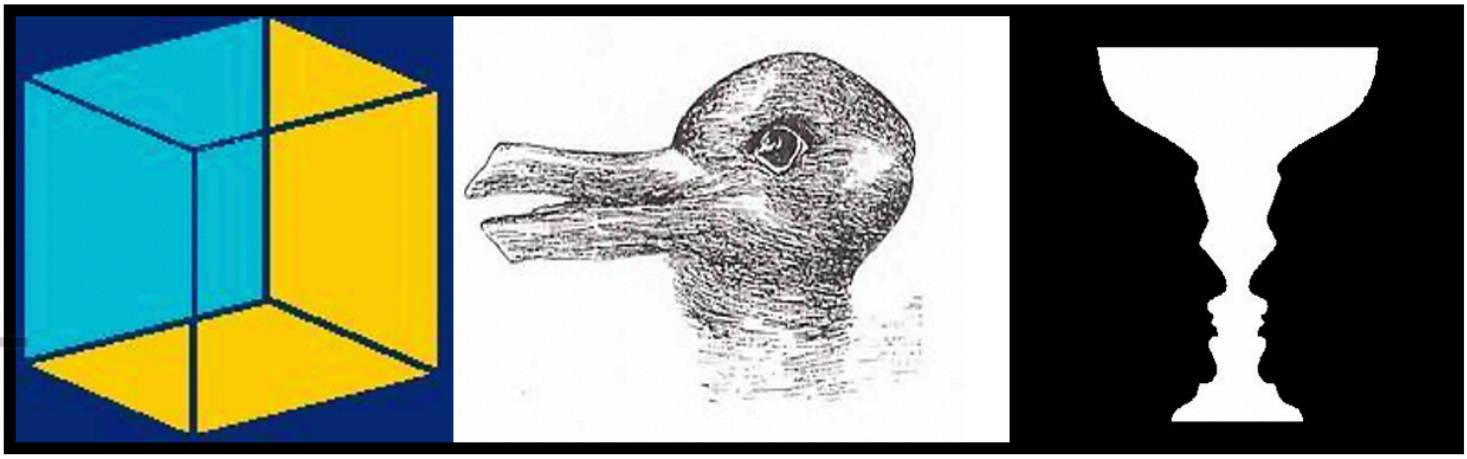
Figure 2. A) Flight arena concept for tethered *Drosophila* flies. Closed-loop control revealed rivalry-like alternating selection of competing visual objects (reproduced from van Swinderen, 2007). B) Independent and alternating eye movements can be seen in (a-d) the sand lance and (e-h) the chameleon (reproduced from Pettigrew, Collin, & Ott, 1999).

Figure 3. Evidence for perceptual rivalry in macaque. *Upper row*: When a transparent sphere speckled with randomly placed black dots is illuminated in a way that it casts a shadow on a screen, observers perceive a two-dimensional, disk-shaped pattern of randomly distributed patches. However, if one rotates the sphere, say on a vertical axis, its two-dimensional projection is readily perceived as the shadow of a rotating three-dimensional sphere thanks to a phenomenon termed the kinetic depth effect, or structure-from-motion. Interestingly, though, the direction of rotation of this shadow-sphere (i.e., whether dots on the front surface of the sphere translate to the left or to the right) is inherently ambiguous. Human observers report random alternations in perceived rotation, accordingly. *Lower row*: Eye movements from a macaque monkey observing this stimulus. The purple trace depicts the horizontal displacement of one of the animal's eyes in degrees of visual angle as a function of time. The black trace below shows the first derivative (i.e., velocity) of the same data. Note that the animal's eye is moving back-and-forth either from left-to-right (in a stereotypical pattern termed optokinetic nystagmus). This is followed by repeated shifts from right-to-left, indicating that the animal perceives similar reversals in perceived rotation as humans (figure adapted from Leopold et al., 2003).

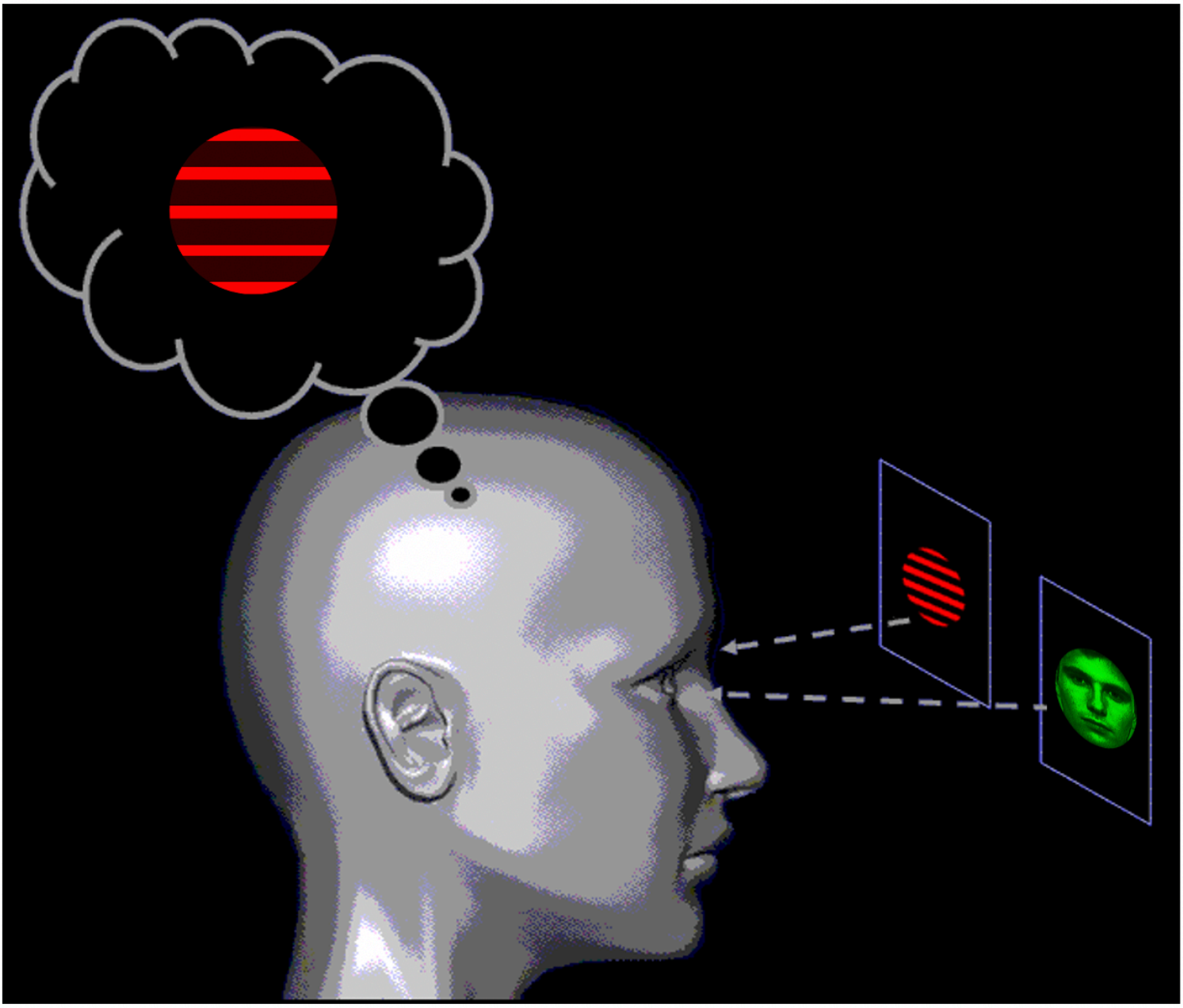
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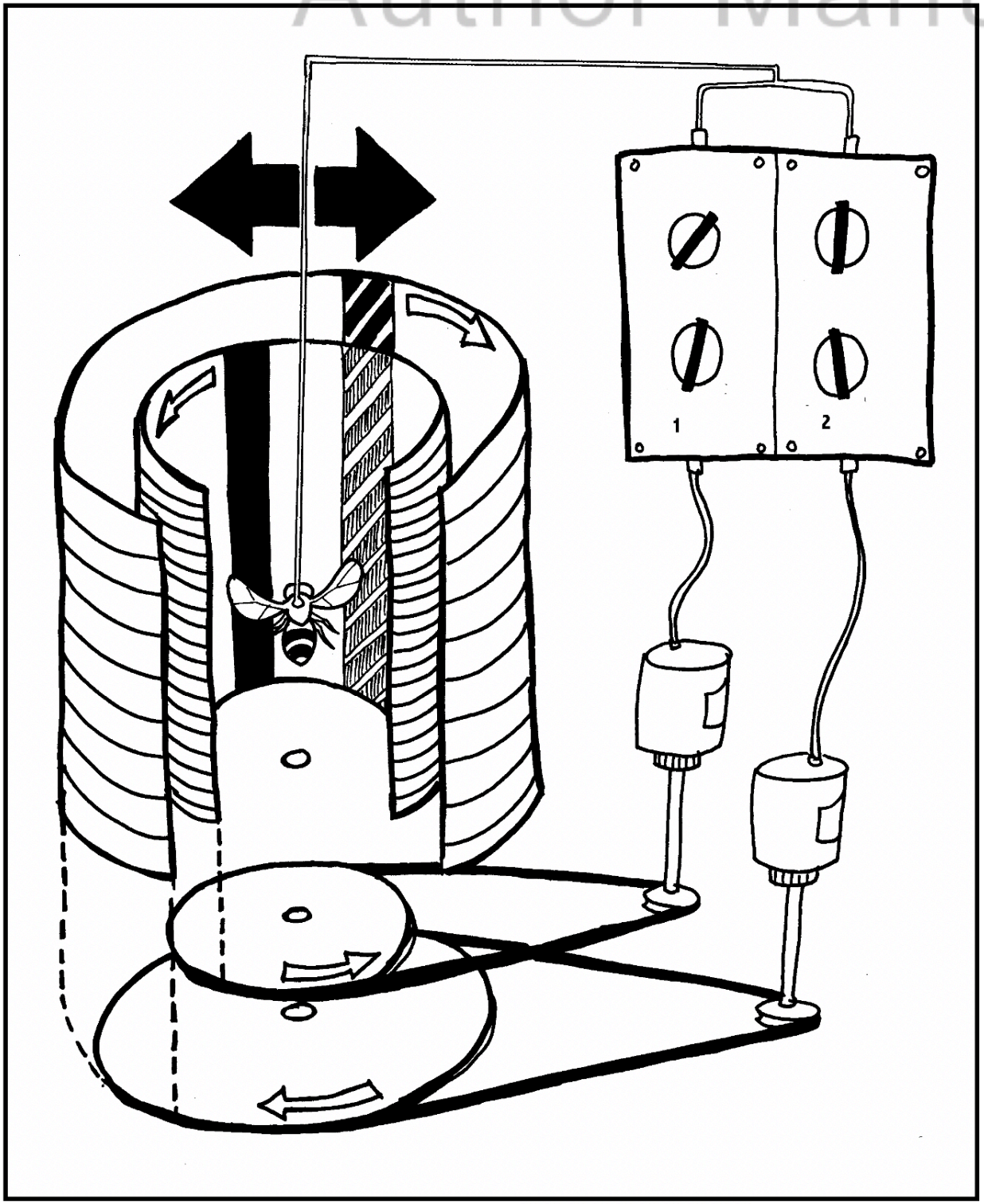


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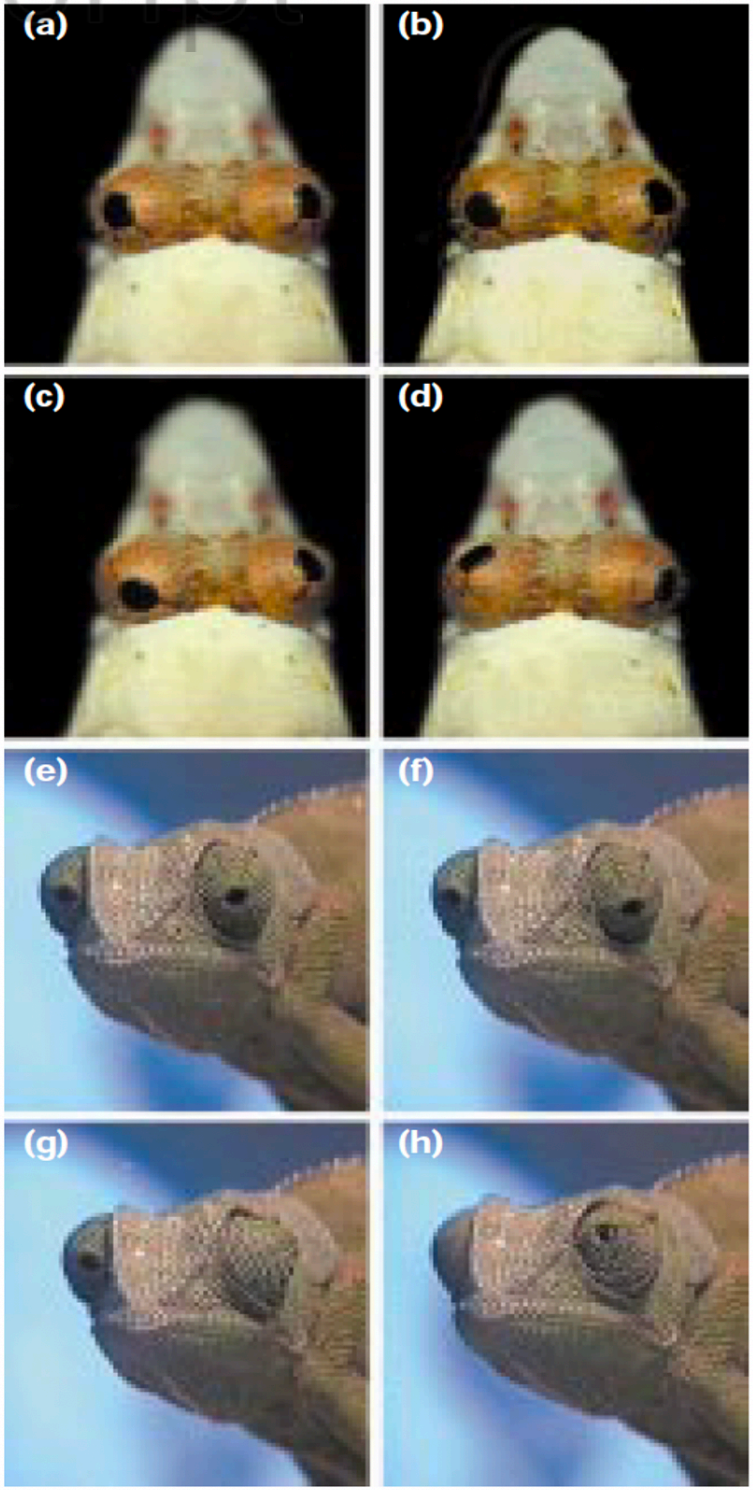
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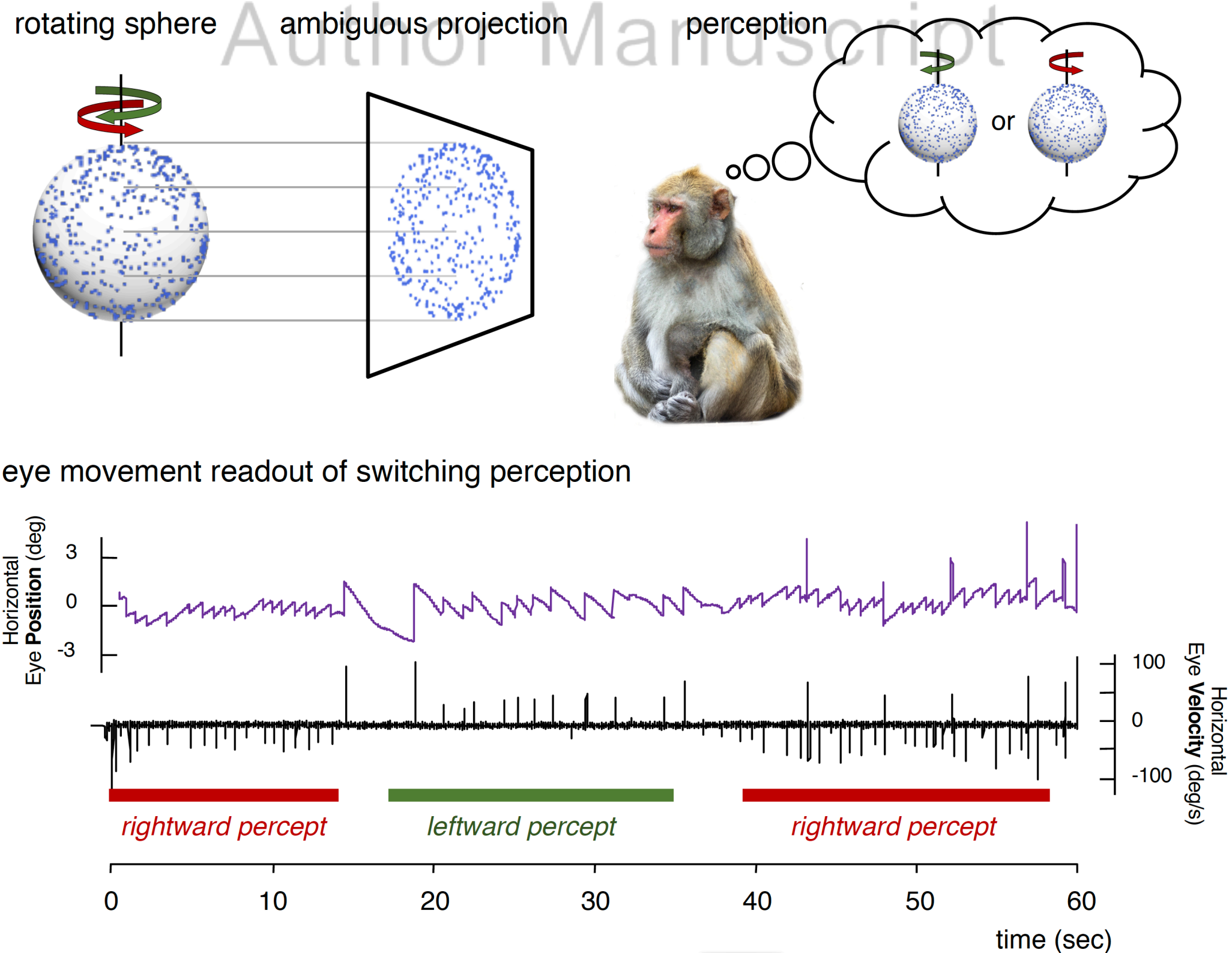


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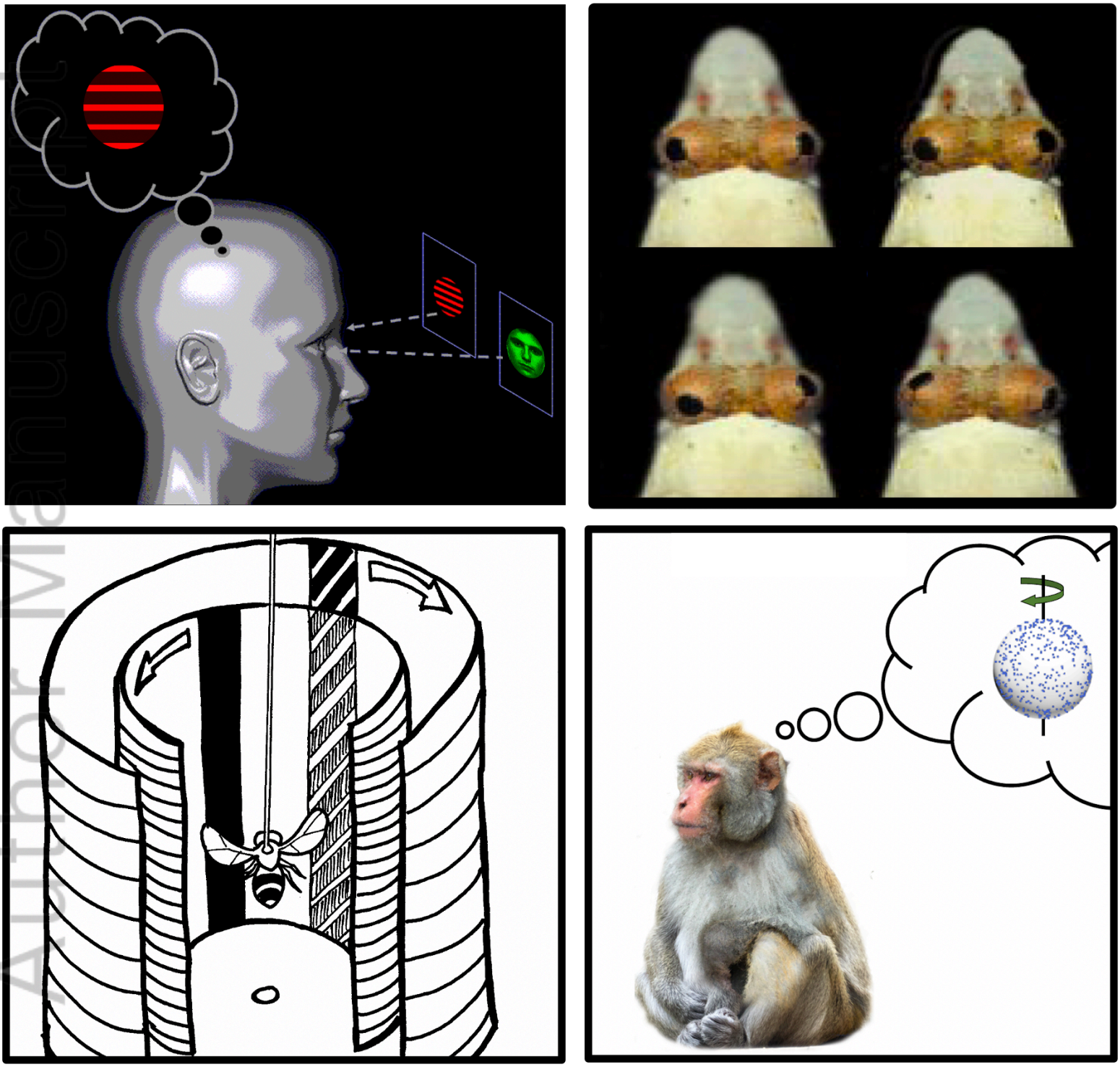


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This review in memoriam of Jack Pettigrew provides an overview of research into the phenomenon of perceptual rivalry, across a wide variety of species including insects, fish, reptiles and primates. Perceptual rivalry is characterized by spontaneous alternations in perceptual state in response to ambiguous or conflicting sensory input. We highlight several interesting commonalities across species and use a comparative approach to better understand how the brain suppresses opposing sensory signals and generates alternations in perceptual dominance.

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