

Knowing by Heart: Visceral Feedback Shapes Recognition Memory Judgments

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Although theories of emotion have long noted the importance of afferent feedback from the autonomic nervous system in generating feelings, there is a growing appreciation that this feedback may also play a role in shaping cognitive experiences. At present, little is known about its functional role in memory judgments. In the current study, we examined whether afferent cardiovascular feedback shapes recognition-memory decisions and experiences when previously encountered faces are being discriminated from novel ones. To investigate this possibility, we capitalized on the natural variation in baroreceptor mediated cardiovascular feedback that is associated with the cardiac cycle, synchronizing the brief presentation of memory probes during retrieval with individual heartbeats. In Experiments 1 and 2, we found that faces presented during cardiac systole (i.e., when visceral feedback is maximal) were more likely endorsed as “old” than those presented during cardiac diastole (i.e., when afferent feedback is minimal). This pattern was present for targets and lures, and held for faces with fearful or neutral expressions. Combining this manipulation with a remember/know procedure, Experiment 3 showed that the influence of afferent cardiovascular feedback is specific to trials on which participants report a feeling of familiarity without successful recollection of pertinent contextual detail. By revealing an influence of baroreceptor mediated cardiovascular feedback on familiarity, the current findings identify the functional role of a specific autonomic channel, previously implicated in emotion, in feeling states that pertain to memory experience.

Keywords: epistemic feelings, recognition memory, cardiovascular feedback, cardiac cycle, dual-process model

The consideration of a role for bodily signals in mental experiences has a long history in academic writing, including James' (1894) influential proposal that emotional experiences may be rooted in the perception of visceral body signals. The empirical investigation of the relationship between changes in the internal state of our body and mental experiences has garnered increasing interest among psychologists and neuroscientists in recent years (for reviews, see Craig, 2009; Critchley & Harrison, 2013; Wiens,

2005). This interest has been fueled by methodological advances in measuring autonomic visceral signals, an increased understanding of pertinent afferent pathways, and the representation of visceral information in the human brain, as well as by the development of theoretical models that elaborate on the role of visceral signals in feeling states (Craig, 2009; Critchley & Harrison, 2013; Damasio & Carvalho, 2013). At present, most of this research has focused on emotion. Yet, there have also been suggestions, and there is mounting empirical evidence, that visceral feedback can influence cognition and decision-making (e.g., Bechara, Damasio, Tranel, & Damasio, 1997; Damasio, 1994; Dunn et al., 2010). In the present study, we will address whether and how such feedback shapes recognition-memory judgments and experiences.

Epistemic Feelings and Recognition Memory

Subjective feeling states that occur in the context of cognitive processing are sometimes referred to as *epistemic feelings* (Moulin & Souchay, 2014), a term that emphasizes their relationship to stored knowledge and online information processing. Examples include the “feeling of familiarity” one may experience when driving through a neighborhood visited long ago (see Gardiner & Richardson-Klavehn, 2000, for a review), the “feeling of knowing,” which arises when stored information cannot be accessed

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with the concurrent impression that it is still available in memory (Hart, 1965; Koriati, 2000; Schwartz, Travis, Castro & Smith, 2000), or “feelings of *déjà vu*,” in which a sense of familiarity is accompanied by the subjective impression that it is false (Brown, 2003; Martin, Fiacconi, & Köhler, 2015; Martin et al., 2012). Such epistemic feelings may not be epiphenomenal but have been suggested to play a functional role in guiding behavior (see Arango-Munoz, 2014, and Moulin & Souchay, 2014, for general reviews). Related conceptual ideas have also been developed in the social cognition literature in the “feelings-as-information” theory (Schwarz, 2012; Schwarz & Clore, 1983), which asserts that some forms of cognitive judgment and decision-making are informed by affective signals that provide a rapid “summary” of the motivational value of the current situation and behavioral choices. By this view, feelings are not a byproduct of cognitive processing, but rather represent a unique source of information that plays an integral role in cognitive functioning.

One cognitive domain in which epistemic feelings have been investigated prominently through empirical research is episodic memory (Tulving, 1985, 2002). Within this domain, much pertinent research has focused on phenomenological experiences that arise in the context of recognition-memory judgments. Interest in these experiences was sparked by Tulving (1985), who distinguished between two qualitatively different phenomenological states. According to Tulving (1985), the experience of “remembering” occurs when recognition of a stimulus is associated with mental-time travel that entails recovery of contextual details about a pertinent past episodic encounter. By contrast, the experience of “knowing” is not associated with successful recovery of any such episodic context. Instead, it involves a mere impression that the current stimulus is “old” and has been encountered before. In this framework, the impression of “knowing” that accompanies some recognition-memory decisions maps onto the phenomenological feeling of familiarity (see Gardiner & Richardson-Klavehn, 2000). The distinction between “remembering” and “knowing” is also central to dual-process models of recognition memory, which elaborate on the relationship between these phenomenological experiences and the retrieval processes of *recollection* and *familiarity assessment*, respectively (see Mayes, Montaldi, & Migo, 2007, and Yonelinas, 2002, for reviews).

Starting with Titchener’s (1910) famous notion of the “warm glow of familiarity,” feelings have been of particular interest toward understanding familiarity. There is a significant body of behavioral work suggesting that repeated stimulus exposure can have positive affective consequences (Bornstein, 1989; Harmon-Jones & Allen, 2001; Zajonc, 1968, 2001). Other research also implicates positive affect in recognition-memory judgments (Duke, Fiacconi, & Köhler, 2014; Garcia-Marques, Mackie, Claypool, & Garcia-Marques, 2004; Goldinger & Hansen, 2005; Monin, 2003; Phaf & Rotteveel, 2005; Verde, Stone, Hatch, & Schnall, 2010). For example, in research with an affective priming paradigm, we recently reported that participants are more likely to endorse faces as “old” when they are preceded by the subliminal masked presentation of faces with a happy as compared to neutral expression (Duke et al., 2014). Most relevant to the present discussion, the effect was specific to recognition decisions that were associated with a sense of familiarity as probed with the remember/know procedure. These types of behavioral findings provide support for a link between feelings of familiarity and positive

affect, as originally proposed by Titchener (1910). However, they do not point to any visceral feedback channel that could mediate this relationship.

A prominent perspective in psychology and the neurosciences holds that afferent visceral signals form a core element of subjective feeling states (Damasio & Carvalho, 2013; James, 1894; Schachter & Singer, 1962). In fact, it has been argued that feelings *are* mental experiences of body states (e.g., Damasio, 1999). Feelings can reference internal states of the body that are related to homeostasis, such as hunger, but they can also reference internal states triggered by external stimulation, such as when one sees a threatening animal or hears the voice of a loved one. The relationship between visceral signals and feeling states has received considerable investigation in the context of emotion, with studies demonstrating, for example, that increases in bodily arousal induced through physical activity (White, Fishbein, & Rutsein, 1981; White & Kight, 1984), administration of pharmacological stimulants (Schachter & Singer, 1962), or modified, false physiological feedback (Gray, Harrison, Wiens, & Critchley, 2007; Valins, 1966) influence expressed feelings. Given the established impact of visceral feedback on feelings in the domain of emotion, the question arises as to whether epistemic feelings, including familiarity, also rely on visceral autonomic feedback. The potential influence of autonomic signals on memory judgments and feelings of familiarity has seen little empirical consideration in research so far, in particular when pertinent stimuli have no apparent emotional content. To our knowledge, only a handful of studies have addressed this relationship in the context of recognition-memory judgments (Jennings & Hall, 1980; Kafkas & Montaldi, 2012; Morris, Cleary, & Still, 2008; Otero, Weekes, & Hutton, 2011). By and large, these studies have employed psychophysiological recordings of skin conductance (SCR; Morris et al., 2008) or pupil dilation (Kafkas & Montaldi, 2012; Otero, Weekes, & Hutton, 2011), examining whether the outcome of recognition decisions is related to differences in autonomic arousal. Although they provide initial evidence that familiarity for words (Morris et al., 2008; Otero et al., 2011) and pictures (Kafkas & Montaldi, 2012) is associated with an increase in autonomic arousal, it is generally difficult to ascertain, based on psychophysiological recordings alone, whether the observed autonomic reactivity constitutes the source of familiarity experiences, or reflects the engagement of effortful search processes that often characterize a persistent sense of familiarity. Indeed, Morris et al. (2008) argued in favor of the latter interpretation of their SCR findings, given that differential signals to previously studied words were observed only when SCR responses beginning at a long latency poststimulus onset (>1.75 s) were considered. However, these findings do not rule out that other autonomic feedback signals that follow a different time course could provide an affective source of recognition judgments.

Cardiovascular Approaches for Examining the Functional Impact of Visceral Feedback

Researchers interested in the role of visceral feedback in behavior have increasingly turned their attention to experimental techniques that focus on cardiac influences, building on well-documented interactions between the cardiovascular system and the central nervous system (see Critchley & Garfinkel, 2015, for a review). Interest in this approach is particularly strong in the

literature on feelings given that heartbeats, unlike some other peripheral autonomic markers, such as pupillary responses, can be directly felt in conscious experience. Cardiac timing paradigms exploit extant knowledge about afferent and efferent pathways between the heart and the brain, and capitalize on the phasic modulation of visceral feedback to the brain that occurs across the cardiac cycle (Lacey & Lacey, 1970, 1978). Because pressure-sensitive arterial baroreceptors fire in bursts every time blood is ejected into the aortic and carotid arteries, feedback from these receptors is present during cardiac systole but not during diastole. These feedback signals are relayed to brainstem structures by the vagus and the glossopharyngeal nerves, and play an important role in the control of blood pressure. Critically, they are also processed in higher order cortical regions that are known to play a role in interoceptive awareness, that is, the conscious perception of the visceral state of the body, including the anterior insula (Craig, 2009; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). The naturally occurring variation in baroreceptor-mediated visceral signaling across the cardiac cycle offers a unique and powerful means to examine how afferent autonomic feedback signals shape stimulus processing. It allows for the synchronization of stimulus presentation with periods in which brain structures are known to receive feedback about individual heartbeats (Gray et al., 2007; Schandry et al., 1986), such that stimuli briefly presented at systole are processed concurrently with baroreceptor signaling whereas stimuli presented at diastole are not. In terms of experimental design, this approach goes beyond the mere recording of autonomic visceral signals. It has some similarity to the experimental approach employed in affective priming paradigms (e.g., Duke et al., 2014), with the added critical feature of implicating a specific autonomic feedback channel for inferences at the mechanistic level.

Much of the extant research exploiting natural phasic variation in baroreceptor-mediated signaling has focused on its influence on sensory processing, with particular emphasis on the perception of pain (Dworkin et al., 1994; Edwards, Inui, Ring, Wang, & Kakigi, 2008; Edwards, Ring, McIntyre, & Carroll, 2001). In fact, only recently has this paradigm been utilized toward understanding the influence of visceral afferent signaling on emotional experience more broadly (Critchley & Garfinkel, 2015; Garfinkel et al., 2014; Gray et al., 2012). Two recent psychophysiological studies that employed a cardiac synchronization approach have confirmed a role for afferent cardiovascular feedback in shaping emotional experience. Specifically, these studies showed that faces depicting expressions of fear or disgust were rated as more intense when presented during cardiac systole than during diastole (Garfinkel et al., 2014; Gray et al., 2012). Notably, the observed increase in intensity ratings of fearful faces at systole was also associated with region-specific changes in brain activity revealed with functional MRI, including increases in amygdala activity (Garfinkel et al., 2014). In a related experiment, Garfinkel et al. demonstrated that detection of fearful faces under challenging attentional demands was enhanced during cardiac systole, suggesting that afferent cardiovascular signals may also boost attention to threatening stimuli. Finally, cardiac timing manipulations have also been employed in research on memory formation for verbal materials (Garfinkel et al., 2013). Examination of subsequent memory performance for detected target words embedded in a stream of rapidly presented distractor words revealed poorer subsequent

recall for target words that had been presented during cardiac systole as compared to diastole at encoding.

The Present Study

In the present study, we focused on the role of visceral autonomic signals at retrieval, aiming to examine whether such signals can inform recognition decisions and shape corresponding phenomenological experiences. For this purpose, we applied the cardiac-timing paradigm in the context of a recognition memory task for faces. Building on the demonstrated influence of cardiac afferent signaling in shaping feeling states in other domains (Garfinkel et al., 2014; Gray et al., 2012), we leveraged phasic variations in baroreceptor-mediated cardiovascular feedback during brief presentation of faces for recognition-memory judgments. We predicted that participants would be more likely to endorse both previously studied and novel faces as “old” when presented during cardiac systole relative to cardiac diastole. Moreover, based on the general notion that affective signals may only shape cognitive decisions and experiences under conditions in which access to other information that could guide the judgment is limited (Schwarz, 2012), we also expected that this differential endorsement rate would be specific to memory decisions that are associated with feelings of familiarity in the absence of perceived success in recall of pertinent episodic detail. Finally, given that affective priming manipulations have been shown to influence recognition decisions even for stimuli with no apparent emotional content (Duke et al., 2014), we anticipated to find these effects even in memory judgments on faces with neutral facial expression.

Experiment 1

To assess the role of cardiac feedback in guiding recognition memory decisions, we employed a recognition memory task for faces of previously unknown (i.e., nonfamous) individuals in combination with psychophysiological recordings of cardiovascular functioning (i.e., electrocardiography [ECG]). This approach allowed for synchronization of the presentation of memory probes with different phases of the cardiac cycle in order to examine the impact of transient increases in afferent cardiovascular feedback on memory judgments. Given that prior research with the cardiac timing paradigm has revealed significant influences on the intensity of perceived fear in judgments of facial expression (Garfinkel et al., 2014; Gray et al., 2012), we started our study using face stimuli with fearful expressions (Experiment 1). Synchronizing the presentation of targets and lures with the cardiac cycle, we expected to observe increased endorsement of items during systole irrespective of whether they had previously been studied or not (see Duke et al., 2014, for further discussion of rationale).

Method

Participants. Thirty-seven undergraduate students from Western University participated in this study in exchange for either course credit, or monetary compensation. There were 23 females, and the mean age was 18.6 years ($SD = 0.96$ years). Sample size was chosen to be similar to that used in other studies employing the cardiac-timing paradigm (see Garfinkel et al., 2014; Gray et al., 2012). For the purpose of conducting an a priori power analysis,

we estimated the effect size of our cardiac timing manipulation based on the results from a recent study that used a similar cardiac timing manipulation to probe for cardiovascular feedback effects on fear intensity judgments (Garfinkel et al., 2014). Based on this prior study, we estimated the effect size of the influence of cardiac timing (i.e., systole vs. diastole) to be $d = .61$. Using this estimated effect size, a power analysis (conducted using G*Power software; Faul, Erdfelder, Lang, & Buchner, 2007) revealed that the required sample size to detect an effect of cardiac timing with a power = 0.8 is 18 participants. Our sample size of 37 participants (Experiments 1 and 2) would therefore yield a power = .98. All experimental procedures were approved by the Non-Medical Research Ethics Board at Western.

Materials. Stimuli consisted of 136 colored images of faces depicting a fearful expression and were acquired from the Karolinska Directed Emotional Faces database and the NimStim Emotional Face Stimuli database (Lundqvist et al., 1998; Tottenham et al., 2009). The faces were cropped using an oval template to remove hair and ears while still maintaining complete coverage of the forehead and jaw (Duke et al., 2014). The full set of 136 faces was split into two sets of 68 faces, with one set serving as the study items, and the other serving as the novel lures during the recognition test. Sets were counterbalanced across participants ensuring that each set was equally likely to be assigned to either the study or lure items. All face stimuli subtended 17° of visual angle, and were presented on a CRT monitor with a refresh rate of 60 Hz.

Psychophysiological recordings. ECG signals were recorded using a BIOPAC MP150 MRI-compatible system (BIOPAC Systems, Goleta, CA) with a BIOPAC ECG100C-MRI amplifier and three Ag/AgCl electrodes. ECG electrodes were attached using the standard three-electrode Lead II configuration. The ECG signal was sampled at 2,000 Hz, amplified, and band-pass filtered from 1 to 35 Hz. To synchronize stimulus presentation during retrieval to the different phases of the cardiac cycle, we used Acknowledge 4.3 software, which allowed for the detection of *R* waves in the ECG

signal in real-time. Once an *R* wave was detected, a digital pulse was transmitted to the experimental computer running Eprime 2.0 software (Psychology Software Tools, Pittsburgh, PA), which triggered stimulus presentation after a specified targeted delay of either 267 or 500 ms for systole and diastole trials, respectively. These timing parameters were similar to those used in prior research examining the influence of baroreceptor-mediated cardiac feedback signals on nociceptive reflexes (Edwards, McIntyre, Carroll, Ring, & Martin, 2002) and were chosen, in line with several prior studies, based on an estimate of the arrival of baroreceptor mediated feedback signals to brainstem nuclei within 250–350 ms following the *R* wave (see Edwards, Ring, McIntyre, Winer & Martin, 2009; Garfinkel et al., 2014; Ring, Liu, & Brener, 1994). Participants were informed that the purpose of the ECG recordings was to monitor physiological changes associated with memory performance, and they were not made aware of the cardiac timing manipulation.

Experimental procedures. After setup of the psychophysiological recordings, participants performed an incidental encoding task in which they were asked to view faces on the screen, one at a time, and rate how much they liked the face on a scale from 1 (*strongly dislike*) to 6 (*strongly like*). Each face was presented for 1.5 s and the participants had 4 s to rate it. Following this response window, there was intertrial interval of approximately 4 s. After completing the incidental encoding task, participants were introduced to our memory test, in which all 68 previously viewed faces were presented intermixed with 68 novel faces. Participants pressed the “1” key if they believed the face had been previously studied or the “2” key if they believed the face to be novel (see Figure 1). Critically, half of the previously studied and novel faces were presented during the systole phase of the cardiac cycle (targeted presentation time at 267 ms after the *R* wave), while the other half were presented during the diastole phase (targeted presentation time at 500 ms after the *R* wave; see Figure 2). Order of cardiac timing conditions was randomized across all 136 trials.

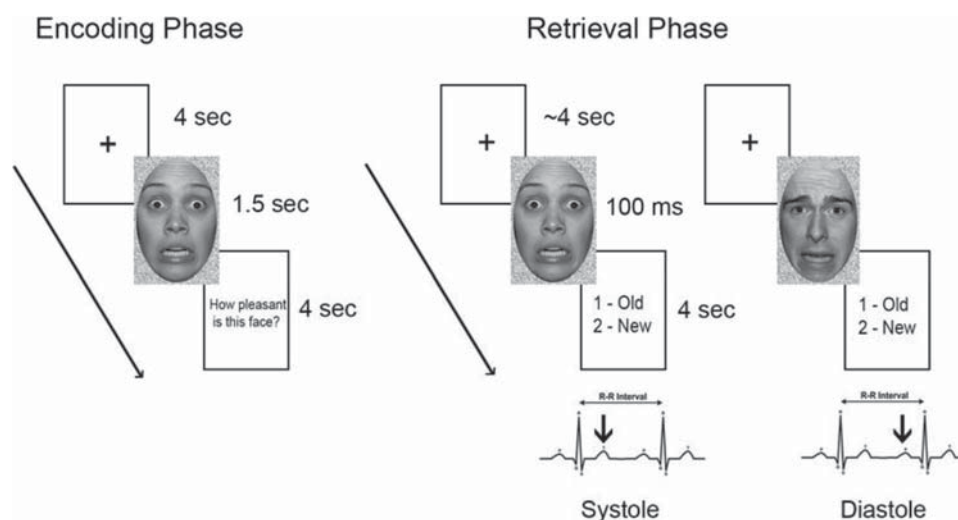


Figure 1. Basic experimental procedure used in Experiment 1. The procedures used in Experiments 2 and 3 were derived from this basic procedure, with response options “old” and “new” replaced by “remember,” “know,” and “new” in the retrieval phase of Experiment 3. Fearful faces were replaced with neutral faces in Experiments 2 and 3.

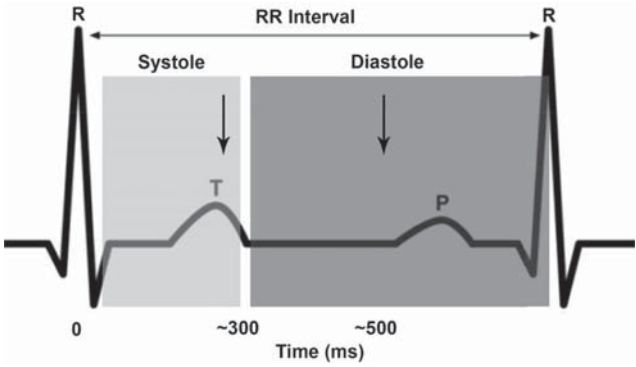


Figure 2. Temporal relationship between phases of the cardiac cycle, electrocardiography signal, and stimulus presentation. Arrows represent targeted stimulus onset times for systole and diastole trials, respectively.

Recognition probes were presented for a short duration of 100 ms to ensure that presentation overlapped closely with central processing of afferent cardiac feedback. Participants were asked to respond with a button press within 4 s following stimulus onset. If no response was provided within this time window, the corresponding trial was discarded from subsequent analyses, and an auditory tone was presented to encourage faster responding on subsequent trials. Presentation of the next stimulus was triggered by the first *R* wave occurring after an intertrial interval of 4 s.

Results and Discussion

Validation of stimulus onset times. Given that targeted stimulus presentations required accurate detection of *R* waves, we first verified this timing based on digital markers of actual presentation time recorded during the test session. Toward this end, we calculated the mean and standard deviation of onset times relative to the preceding recorded *R* wave in each phase of the cardiac cycle for each participant, which were then averaged across our entire sample. In line with our targeted timing parameters, the mean stimulus onset time was 283 ms ($SD = 3$ ms) for systole trials, and was highly consistent within individuals ($M_{SD} = 9$ ms, $SD_{SD} = 2$ ms). Similarly, accuracy ($M_{onset\ time} = 518$ ms, $SD = 3$ ms) and consistency ($M_{SD} = 10$ ms, $SD_{SD} = 6$ ms) of onset times for diastole trials were close to the targeted values. Moreover, stimulus presentation during diastole trials always fell within the targeted *R*–*R* interval, indicating that onset times for these trials were not unduly affected by normal beat-to-beat variability in the time between successive *R* waves.

Recognition memory performance. To examine the influence of cardiac timing on memory performance, we calculated the mean proportion of “old” responses to both previously studied and new items, for each cardiac-timing condition (see Figure 3). We primarily focused on this measure because our predictions were concerned with effects of cardiac cycle on endorsement rates rather than accuracy. These scores were submitted to a repeated measures analysis of variance (ANOVA) with Item Status (old/new), and Cardiac Timing (systole/diastole) as within-subjects factors. This analysis revealed a significant main effect of Item Status, $F(1, 36) = 39.1$, $p < .001$, $\eta_p^2 = .52$, with a greater proportion of “old” responses given to old as compared to new

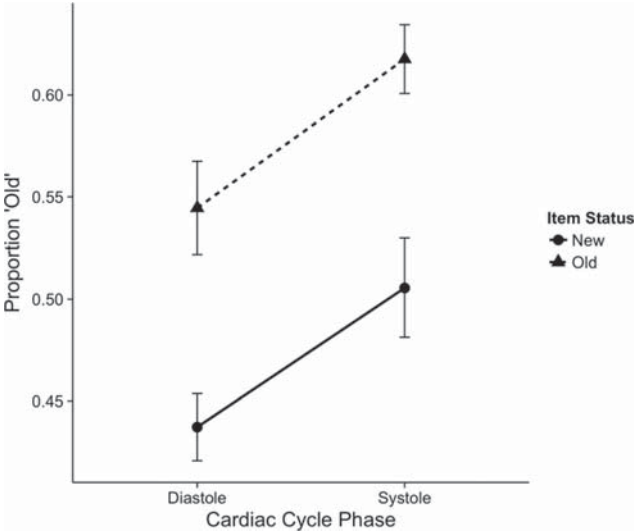


Figure 3. Mean proportion of “old” responses for old and new items as a function of item presentation during cardiac systole and diastole in Experiment 1. Error bars represent standard error of the mean corrected for within-participants comparisons (Morey, 2008).

items, indicating that participants accurately discriminated between previously studied and novel recognition probes at above-chance level. Consistent with our prediction that cardiovascular feedback influences recognition-memory decisions, there was also a main effect of Cardiac Timing, $F(1, 36) = 8.52$, $p = .006$, $\eta_p^2 = .19$; specifically, participants were more likely to endorse memory probes as “old” when these probes were presented at systole. There was no significant interaction between these variables, $F(1, 36) = .02$, $p = .90$, $\eta_p^2 = .00$, suggesting that the cardiac timing manipulation did not influence targets and lures differentially. Indeed, when we calculated a measure of memory discrimination based on signal-detection theory (d') separately for systole and diastole trials (see Table 1), Cardiac Timing was not found to influence discrimination accuracy, $t(36) = .37$, $p = .72$, $d = .09$. Instead, the increased endorsement rate for probes presented during systole

Table 1
Mnemonic Discrimination (d') and Response Criterion (c)
Values for Experiments 1–3

Experiment	Discrimination (d')		Response criterion (c)	
	Systole	Diastole	Systole	Diastole
Experiment 1	.33 (.47)	.29 (.44)	–.20 (.53)	.00 (.42)
Experiment 2	.29 (.39)	.40 (.39)	–.09 (.36)	.08 (.35)
Experiment 3				
“Remember”	.45 (.53)	.64 (.53)	1.21 (.60)	1.10 (.50)
“Know”				
Uncorrected	.18 (.44)	.25 (.51)	.15 (.47)	.28 (.50)
Corrected	.39 (.52)	.54 (.48)	–.11 (.50)	.00 (.57)

Note. Values for Experiment 3 are depicted separately for “remember” and “know” trials. For “know” trials, we calculated the values of each parameter using both the raw uncorrected response proportions and the corrected proportions based on the independence assumption (Yonelinas, 2002). Numbers in parentheses reflect SD .

was reflected in a shift in response bias (c) for these trials, $t(36) = 2.77$, $p = .008$, $d = .42$.

Experiment 2

The results of Experiment 1 provide evidence in support of the idea that cardiac afferent feedback influences recognition memory decisions for fearful faces. However, the experiment does not address whether this influence is limited to conditions in which the stimuli judged display emotional expressions. As reviewed in the introduction, our theoretical framework for the current study emphasizes a broader link between visceral feedback and memory experiences at the time of retrieval, allowing for the prediction that the influence of cardiac timing should not be restricted to memory judgments for fearful stimuli, and should also be present for stimuli that have no apparent emotional content. In Experiment 2, we tested this idea by employing faces with neutral expressions while keeping all other aspects of the procedure identical to Experiment 1. We expected that the pattern of results obtained with the cardiac-timing manipulation would be the same as that observed in Experiment 1.

Method

Participants. Thirty-seven undergraduate students from the Western University participated in this study in exchange for either course credit, or monetary compensation. There were 24 females, and the mean age was 18.4 years ($SD = 0.59$ years). Sample size was determined based on Experiment 1, and on prior work employing the cardiac timing paradigm (see Garfinkel et al., 2014; Gray et al., 2012). All experimental procedures were approved by the Non-Medical Research Ethics Board at Western.

Materials. Stimuli consisted of 136 colored images of faces depicting a neutral emotional expression, which were acquired from the same databases as in Experiment 1. These databases provide a category of neutral facial expressions based on normative ratings. All other aspects of stimulus preparation, presentation, and assignment were identical to those in Experiment 1.

Psychophysiological recordings. The psychophysiological setup was identical to Experiment 1.

Experimental procedures. All experimental procedures were identical to Experiment 1.

Results and Discussion

Validation of stimulus onset times. As in Experiment 1, we first verified that our stimulus onset times, relative to the preceding R wave in the ECG signal, were executed as intended. Again, the mean stimulus onset times for systole trials fell within the targeted time window ($M_{\text{onset time}} = 281$ ms, $SD = 4$ ms), and were highly consistent within and across individuals ($M_{SD} = 9$ ms, $SD_{SD} = 1$ ms). Similarly, precision ($M_{\text{onset time}} = 516$ ms, $SD = 4$ ms) and consistency ($M_{SD} = 9$ ms, $SD_{SD} = 1$ ms) of onset times were also high for diastole trials. Again, stimulus presentation during diastole trials always fell within the targeted R – R interval.

Recognition memory performance. As in Experiment 1, we calculated the mean proportion of “old” responses to previously studied and new items for the two stimulus-presentation conditions in relation to cardiac timing (see Figure 4). A repeated measures

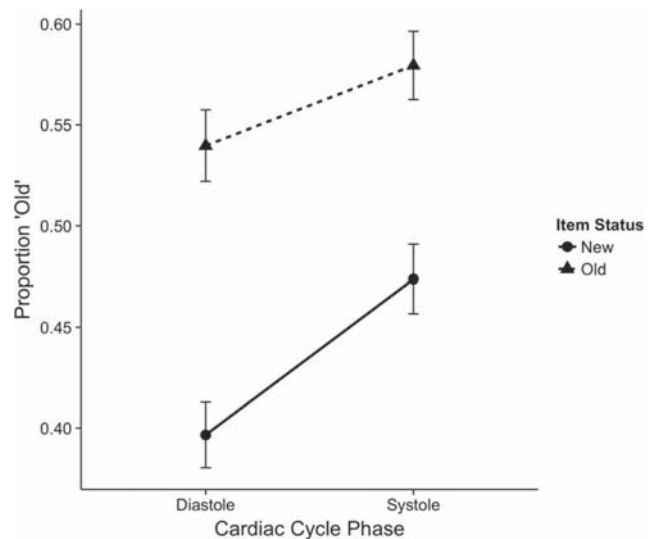


Figure 4. Mean proportion of “old” responses for old and new items, as a function of item presentation during cardiac systole and diastole in Experiment 2. Error bars represent standard error of the mean corrected for within-participants comparisons (Morey, 2008).

ANOVA with Item Status (old/new), and Cardiac Timing (systole/diastole) as within-subjects factors revealed a significant main effect of Item Status, $F(1, 36) = 54.1$, $p < .001$, $\eta_p^2 = .60$, with a greater proportion of “old” responses given to old as compared to new items. Critically, we also found a main effect of Cardiac Timing, $F(1, 36) = 10.20$, $p = .003$, $\eta_p^2 = .22$, showing, as predicted, that participants were more likely to endorse memory probes as “old” when these probes were presented at systole. There was no significant interaction between these variables, $F(1, 36) = 1.42$, $p = .24$, $\eta_p^2 = .04$. Similar to Experiment 1, when we assessed whether discrimination accuracy (as reflected in d') was affected by the cardiac-timing manipulation, we found no evidence for an effect, $t(36) = 1.25$, $p = .22$, $d = .28$ (see Table 1). Instead, the change in endorsement rates was reflected in a shift in response bias (c) for probes presented at systole, $t(36) = 3.14$, $p = .003$, $d = .46$. Together, these results reveal the same pattern of behavior in relation to cardiac timing as reported in Experiment 1. They extend the findings from this experiment by revealing that the influence of afferent cardiovascular feedback on recognition-memory decisions is not limited to judgments about emotional stimuli but applies to faces with neutral expressions as well.

Experiment 3

The findings of Experiments 1 and 2 provide converging support for the notion that afferent cardiovascular feedback can shape recognition-memory decisions. However, these experiments do not address whether the influence of such feedback is tied to specific mnemonic experiences that occur in association with item endorsement. In Experiment 3, we examined whether the influence of cardiovascular feedback is specifically tied to the type of memory experience that is often referred to as feeling, that is, impressions of familiarity. To answer this question, we modified the experimental procedure of Experiment 2 by incorporating remember/

know judgments as part of the recognition-memory task (Tulving, 1985). This procedure allowed us to probe the phenomenology associated with participants' recognition decisions on each trial. We assumed that "know" responses denote phenomenological impressions of familiarity that are distinct from recollective experiences, and that these two types of mnemonic experiences are mutually exclusive (Gardiner, Ramponi, & Richardson-Klavehn, 1998). Following the general notion that affect may primarily inform cognitive decisions under conditions in which access to other information that could guide the judgment at hand is limited (Schwarz, 2012; see Duke et al., 2014, for pertinent findings on recognition memory), we predicted that cardiovascular feedback would influence recognition decisions that are accompanied by impressions of familiarity but not those that are associated with perceived successful recall of episodic detail about the pertinent past stimulus encounter. In other words, we predicted an increase in the proportion of "know" responses to recognition probes presented during cardiac systole as compared to diastole, with no parallel effect for "remember" responses.

Method

Participants. Thirty-four undergraduate students from Western University participated in this study in exchange for either course credit, or monetary compensation. There were 28 females, and the mean age was 22.4 years ($SD = 3.23$ years). Sample size was determined based on Experiment 1, and on prior work employing the cardiac timing paradigm (see Garfinkel et al., 2014; Gray et al., 2012). All experimental procedures were approved by the Non-Medical Research Ethics Board at Western.

Materials. Stimuli were identical to those used in Experiment 2.

Psychophysiological recordings. The psychophysiological setup was identical to Experiment 2.

Experimental procedures. The experimental procedure was identical to that in Experiment 2 except two changes. First, there was an added requirement for participants to make remember/know judgments on the memory probes they deemed "old" in the recognition-memory task. This requirement was implemented in a one-step procedure, such that participants had three response options on each trial: "remember," "know," or "new." They indicated their response by pressing keys 1–3, respectively. Detailed instructions were given describing the distinction between "remember" and "know" judgments (following Rajaram, 1993). Specifically, participants were told that they were to make a "remember" response only if the recognition probe triggered a conscious recollection of contextual information regarding the initial encounter with that item. By contrast, participants were instructed to provide a "know" response when the probe simply felt familiar and did not bring to mind any pertinent contextual information. Participants were given examples of what constituted each response type, and they performed five practice trials on which the experimenter solicited justification for their response. The second aspect of the procedure that was different from Experiment 2 was that, at study, each stimulus was presented three times rather than once only, with repetitions randomly intermixed among other items and a presentation duration of 2 s each. This change was introduced to ensure that the number of trials eliciting "remember" judgments would be sufficiently large to allow for statistical comparisons between

experimental conditions. (Initial pilot work suggested that a single presentation at study led to recognition-judgments that were almost exclusively characterized as "know" responses).

Results and Discussion

Validation of stimulus onset times. As in Experiment 1 and 2, we first verified the precision of our stimulus onset times relative to the preceding *R* wave in the ECG signal. Again, the mean stimulus onset times for systole trials fell within the targeted time window ($M_{\text{onset time}} = 280$ ms, $SD = 3$ ms), and were highly consistent within and across individuals ($M_{SD} = 9$ ms, $SD_{SD} = 1$ ms). Precision ($M_{\text{onset time}} = 515$ ms, $SD = 3$ ms) and consistency ($M_{SD} = 12$ ms, $SD_{SD} = 10$ ms) of onset times were also high for diastole trials. Again, stimulus presentation during diastole trials always fell within the targeted *R*–*R* interval.

Recognition memory performance. Given that our primary interest was in determining whether cardiovascular feedback plays a specific role in shaping impressions of familiarity in recognition-memory judgments, we focused our analyses on the raw proportions of "know" and "remember" responses. Although we recognize that the proportion of "know" responses is often corrected in related research to honor the assumption of independence adopted by many dual-process models (e.g., Jacoby, 1991; Yonelinas, 2002; see Mayes et al., 2007, for discussion), we note that this approach is typically taken when the primary focus is on understanding familiarity and recollection as distinct retrieval processes. Here, we remain agnostic with respect to this issue, using the categories of "remember" and "know" responses to refer to different phenomenological memory experiences. However, in the interest of providing a comprehensive picture, we also report standard signal-detection measures of discrimination (d') and response bias (c) where appropriate, using "know" responses to calculate familiarity estimates with and without correction for independence. In the former case, values were calculated by expressing the proportion of "know" responses as a proportion of trials that were not given a "remember" response (i.e., $1 - R$) for both old and new items (Jacoby, 1991; Yonelinas, 2002).

The mean proportions of the different types of recognition responses as a function of the cardiac-timing manipulation are depicted in Figure 5. As predicted, participants were more likely to make a "know" judgment when recognition probes were presented during cardiac systole than diastole, $t(33) = 2.61$, $p = .014$, $d = .29$. By contrast, there was no effect of the cardiac timing manipulation for "remember" responses, $t(33) = 1.02$, $p = .32$, $d = .14$; in fact the proportion of "remember" responses was numerically lower on systole than on diastole trials (see Figures 5 and 6). To examine the influence of our manipulation in more detail, we also calculated the mean proportion of "remember" and "know" responses given to old and new items separately, as a function of cardiac timing (see Figure 7). A repeated-measures ANOVA with Response (remember/know), Item Status (old/new), and Cardiac Timing (systole/diastole) as within-subjects factors revealed a significant main effect of Item Status, $F(1, 33) = 88.5$, $p < .001$, $\eta_p^2 = .73$, with previously studied items being more likely to be endorsed as "remember" or "know" (i.e., as old) than new items. There was also a main effect of Response, $F(1, 33) = 41.5$, $p < .001$, $\eta_p^2 = .55$, such that participants provided more "know" responses overall. Critically, this analysis also yielded a significant

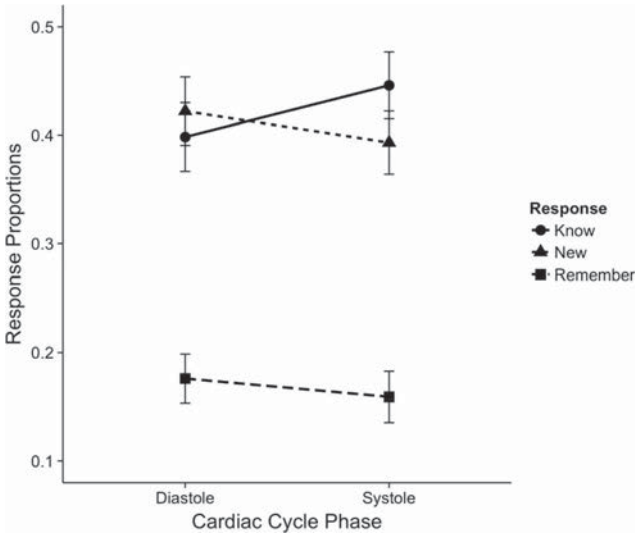


Figure 5. Proportion of different response types given for items presented during cardiac systole and diastole in Experiment 3. Error bars represent standard error of the mean corrected for within-participants comparisons (Morey, 2008).

interaction between Response and Cardiac Timing, $F(1, 33) = 5.65$, $p = .023$, $\eta_p^2 = .15$, indicating that the effect of presentation time differed across “remember” and “know” responses. No other main effects or interactions reached significance (all $ps > .15$). To unpack this Response $\times$ Cardiac Timing interaction, we conducted two separate repeated measures ANOVAs with Item Status (old/new) and Cardiac Timing (systole/diastole) as within-subjects factors for trials associated with “remember” and “know” responses.

For trials on which participants gave a “know” response, there was a significant main effect of Item Status, $F(1, 33) = 16.6$, $p < .001$, $\eta_p^2 = .33$, with a greater proportion of “know” responses provided for old than new items, suggesting above-chance mnemonic discrimination in trials that were associated with a familiarity experience. Critically, there was also a significant main effect of Cardiac Timing, $F(1, 33) = 6.83$, $p = .013$, $\eta_p^2 = .17$, such that participants were more likely to give a “know” response when the recognition probe was presented at systole. This effect was present as a shift in response bias (c) when probed with measures derived from signal detection theory, regardless of whether these measures were based on raw proportions, $t(33) = 2.49$, $p = .009$, $d = .27$, or proportions that were corrected for process-independence (Jacoby, 1991; Yonelinas, 2002), $t(33) = 1.77$, $p = .043$, $d = .21$ (see Table 1). This latter finding provides direct support for our hypothesis that afferent cardiovascular feedback influences recognition decisions that are associated with familiarity experiences. No interaction between Cardiac Timing and Item Status emerged, $F(1, 33) = .046$, $p = .83$, $\eta_p^2 = .001$. As in Experiments 1 and 2, we also found no effect of Cardiac Timing on mnemonic accuracy for familiarity-based responses regardless of whether we considered uncorrected, $t(33) = .68$, $p = .50$, $d = .11$, or corrected, $t(33) = 1.47$, $p = .15$, $d = .25$, discrimination (d') values (See Table 1).

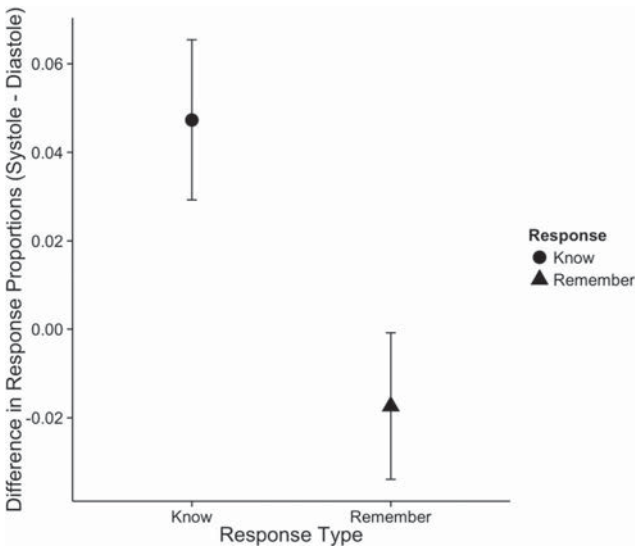


Figure 6. Mean difference in response proportions (systole – diastole) for “remember” and “know” trials, collapsed across old and new items. Error bars represent standard error of the mean difference scores.

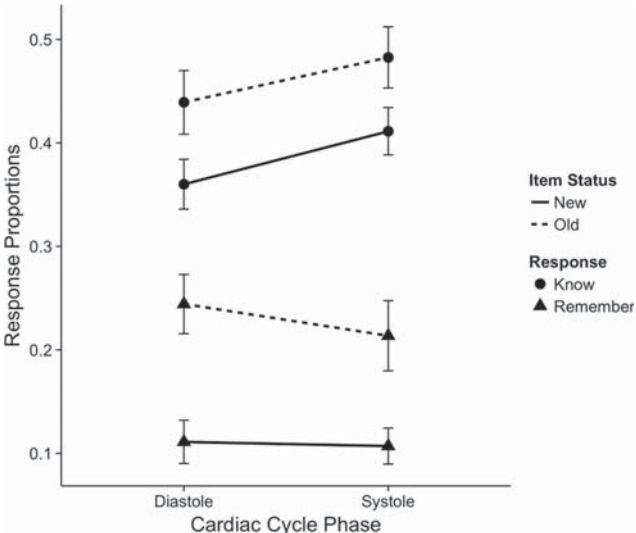


Figure 7. Top section: Mean proportion of “know” responses to old and new items as a function of item presentation during cardiac systole and diastole in Experiment 3. Bottom section: Mean proportion of “remember” responses to old and new items as a function of item presentation during cardiac systole and diastole in Experiment 3. Error bars represent standard error of the mean corrected for within-participants comparisons (Morey, 2008).

For trials on which participants gave a “remember” response, mnemonic accuracy for “remember” trials was also found to be greater than chance, as evidenced by a significant main effect of Item Status, $F(1, 33) = 43.5$, $p < .001$, $\eta_p^2 = .57$, with more “remember” responses given to old as compared to new items. Contrasting with our findings for “know” responses, there was no evidence for an effect of Cardiac Timing for “remember” responses, $F(1, 33) = 1.10$, $p = .30$, $\eta_p^2 = .03$. Moreover, there was no significant interaction between Cardiac Timing and Item Status,

no interaction between Cardiac Timing and Item Status, $F(1, 33) = .046$, $p = .83$, $\eta_p^2 = .001$. As in Experiments 1 and 2, we also found no effect of Cardiac Timing on mnemonic accuracy for familiarity-based responses regardless of whether we considered uncorrected, $t(33) = .68$, $p = .50$, $d = .11$, or corrected, $t(33) = 1.47$, $p = .15$, $d = .25$, discrimination (d') values (See Table 1).

$F(1, 33) = .84$, $p = .37$, $\eta_p^2 = .02$, nor was there an effect of Cardiac Timing on mnemonic accuracy or response bias for “remember” responses when expressed as d' (see Table 1), $t(33) = 1.61$, $p = .11$, $d = .28$, and c , $t(33) = 1.48$, $p = .15$, $d = .20$, respectively. Considered together, these results support our hypothesis that afferent cardiovascular feedback influences recognition decisions that are associated with experiences of familiarity but not those associated with recollective experiences. As such, our findings reveal a striking specificity regarding the influence of cardiovascular feedback on memory judgments.

General Discussion

Guided by the perspective that feeling states are typically shaped by afferent visceral feedback, the current study sought to examine whether baroreceptor mediated cardiovascular feedback influences epistemic feelings in the context of recognition memory judgments. We probed the contribution of this feedback to memory decisions and corresponding experiences by synchronizing the presentation of recognition probes with different phases of the cardiac cycle. In Experiments 1 and 2, we demonstrated for the first time that such signaling can indeed shape recognition memory decisions for faces with fearful and neutral emotional expressions, respectively. These experiments revealed that the presence of afferent cardiovascular signaling increases the likelihood with which participants endorse recognition probes as previously studied. In Experiment 3, we combined our cardiac timing manipulation with remember/know judgments (Tulving, 1985) to determine whether the influence of cardiovascular feedback is specific to recognition decisions that are associated with feelings of familiarity. Indeed, we found that afferent cardiac signaling boosted endorsement of recognition probes as “old” on trials for which participants reported a feeling of familiarity but not on trials that were accompanied by a recollective experience. By revealing this influence of baroreceptor-mediated cardiac feedback on feelings of familiarity, our study shows that epistemic feelings bear a core resemblance to other affective states.

Relationship to Previous Research on Familiarity and Autonomic Arousal

Although prior research on the role of visceral feedback in shaping epistemic feelings is sparse, a handful of studies have used psychophysiological measures of autonomic arousal to probe autonomic reactivity during recognition memory tasks (Morris et al., 2008; Kafkas & Montaldi, 2012; Otero et al., 2011; Vö et al., 2008). The findings reported in these studies generally align in demonstrating that previously studied items elicit an increase in autonomic arousal as assessed using pupillometry (Kafkas & Montaldi, 2012; Otero et al., 2011; Vö et al., 2008), and skin conductance responses (Morris et al., 2008). Of particular relevance for the current investigation, two of these studies examined changes in autonomic arousal in relation to the subjective experience associated with recognition memory decisions for pictures (Kafkas & Montaldi, 2012) and words (Otero et al., 2011) using the remember/know task. Both of these studies reported a considerably larger increase in pupil diameter for items associated with “remember” responses as compared to items deemed novel, with items assigned a “know” response eliciting an intermediate pupil dilation re-

sponse. Converging evidence for a link between perceived oldness and autonomic arousal was provided by Morris et al. (2008), who found that brief, masked presentations of previously studied words elicited a larger skin conductance response than did novel words. Although these findings point to a link between autonomic arousal and feelings of familiarity, they do not establish whether the observed changes in arousal reflect the source of feelings of familiarity or the outcome of effortful retrieval processing (see Morris et al., 2008). Moreover, the relative increase in pupil diameter for items associated with a “remember” as compared to a “know” response (Kafkas & Montaldi, 2012; Otero et al., 2011) casts doubt on the notion that the autonomic signals reflected in pupillary measures are specifically tied to the subjective impression of familiarity. By focusing on aspects of autonomic functioning that can be directly felt as part of subjective experience, that is, individual heartbeats, the current study, in contrast, revealed a source of visceral feedback that is specifically tied to epistemic feelings of familiarity. Building on the phasic variation in baroreceptor-mediated feedback that characterizes the cardiac cycle, our experimental approach also allowed us to overcome some of the inferential limitations that are associated with paradigms that solely rely on recordings, and to form initial conclusions regarding the direction of influence. In line with directional inferences drawn in many other studies based on the cardiac timing paradigm (Dworkin et al., 1994; Edwards, Inui, Ring, Wang, & Kakigi, 2008; Edwards, Ring, McIntyre, & Carroll, 2001; Garfinkel et al., 2014; Gray et al., 2012; Pramme, Larra, Schächinger, & Frings, 2014), we interpret the current findings to suggest that baroreceptor-mediated signaling informs memory decisions and shapes experiences of familiarity.

A Role for Cortical Inhibition in Cardiac Timing Effects on Behavior?

In research with the cardiac timing paradigm in the domain of sensory and pain processing, it has been suggested that afferent baroreceptor signals directly influence cortical processing (see Duschek, Werner, & Reyes Del Paso, 2013, for a review). This contention is based on studies using electroencephalography recordings to examine evoked cortical potentials in response to artificial baroreceptor stimulation (Elbert & Rau, 1995; Rau, Pauli, Brody, Elbert, & Birbaumer, 1993). Specifically, these studies reported a reduction in the amplitude of the contingent negative variation potential during baroreceptor stimulation, suggesting that such stimulation is associated with a decrease in cortical excitability. Such findings have led some researchers to conclude that afferent baroreceptor signaling may result in increased cortical inhibition (Elbert & Rau, 1995; Rau et al., 1993). Related research on the functional impact of such signals has also often adopted this perspective, showing a reduction in pain sensitivity and an attenuation of spinal reflexes in association with increased baroreceptor-mediated cardiac feedback (Dworkin et al., 1994; Edwards et al., 2008; Edwards et al., 2001). In research on emotion and cognitive judgments, however, several findings have recently emerged that cast doubt on the notion that afferent baroreceptor feedback is ubiquitously associated with a dampening of cortical excitability and a corresponding inhibition in behavior (Garfinkel et al., 2014; Gray et al., 2012; Park, Correia, Ducorps, & Tallon-Baudry, 2014). For example, two studies with the cardiac timing

paradigm have revealed an increase in perceived intensity of facial expressions of fear and disgust during systole as compared to diastole (Garfinkel et al., 2014; Gray et al., 2012). Similarly, other studies have demonstrated better detection of near-threshold visual stimuli in association with an increase in prestimulus heartbeat evoked neural activity, and improved detection of emotional stimuli under high attentional demands at systole (Garfinkel et al., 2014; Park et al., 2014). Given that, in the current study, the presentation of stimuli that coincided with heightened afferent baroreceptor signaling increased the likelihood for such stimuli to be endorsed as previously studied, the present results add to the growing body of evidence that refutes the notion that baroreceptor-mediated signaling always has an inhibitory effect on the processing of sensory stimuli. The reported functional specificity with respect to experiences of familiarity further complicates an account of the present findings with reference to inhibition. While our findings do not discredit the interpretation of prior results in studies on pain and some other domains of sensory processing in terms of inhibition, they do call for further research that will reveal the specific sensory and task conditions under which inhibition is operant in cardiac-timing paradigms.

Relationship Between Visceral Feedback and Attribution Theories of Familiarity

The demonstrated role for visceral feedback in shaping familiarity-based recognition decisions is of particular interest in the context of the attribution framework developed by Jacoby and colleagues for understanding familiarity (Jacoby & Dallas, 1981; Jacoby, Kelley, & Dywan, 1989). This framework assumes that feelings of familiarity in recognition memory tasks are not necessarily a property of stored memory traces, but can instead result from a heuristic process whereby participants evaluate the perceptual or conceptual fluency (i.e., subjective ease of processing) that is associated with the memory probe, and then use this information to make an inference regarding prior exposure. Evidence in favor of this account stems from studies demonstrating that experimental manipulations that artificially enhance ease of processing of recognition probes can increase feelings of familiarity for those items (Duke et al., 2014; Jacoby & Whitehouse, 1989). Prior research on fluency has also implicated positive affect in this attribution. In fact, some have argued that processing fluency in itself is hedonically marked (Harmon-Jones & Allen, 2001; Reber, Winkielman, & Schwarz, 1998; Willems, van der Linden, & Bastin, 2007; Winkielman & Cacioppo, 2001; Winkielman, Schwarz, Fazendeiro, & Reber, 2003; Zajonc, 2001). Based on the present findings, we suggest that autonomic signals play an important role in attribution in familiarity-based recognition judgments. Considered within an attribution account, when recognition probes are presented during cardiac systole, participants may interpret the transient increase in arousal that results from baroreceptor mediated feedback as owing to the familiarity of the stimulus probe. That we observed the cardiac timing effect on memory decisions even for novel lures in the three experiments reported here can be seen as particularly strong support for a role of attribution in the phenomenon under study (see Duke et al., 2014; Jacoby & Whitehouse, 1989; and Verde et al., 2010, for further discussion). This interpretation is also in line with conclusions drawn in research on emotion based on demonstrations that experimentally induced

increases in bodily arousal through physical activity (White et al., 1981; White & Kight, 1984), administration of pharmacological stimulants (Schachter & Singer, 1962), or false physiological feedback (Gray, Harrison, Wiens, & Critchley, 2007; Valins, 1966) can be misattributed to feeling states.

The discrepancy-attribution framework proposed by Whittlesea and colleagues (Whittlesea, 1997; Whittlesea & Williams, 1998, 2000) extends the perspective forwarded by Jacoby and others (Jacoby & Dallas, 1981; Jacoby et al., 1989) by positing that increases in fluency are especially likely to be attributed to prior experience when they are perceived as surprising or discrepant with one's expectations based on contextual norms. This account emphasizes the critical importance of expectancy violations in feelings of familiarity; it was proposed to explain why we may experience a particularly strong feeling of familiarity when we encounter the butcher on the bus, but do not experience this same familiarity when we interact with him in the butcher shop (Mandler, 1980; Whittlesea & Williams, 1998). The current demonstration of a role of visceral feedback in feelings of familiarity is of particular interest in this context given that expectations and predictions have recently also been proposed to sculpt subjective experience based on interoception of autonomic signals (Barrett & Simmons, 2015; Seth, Suzuki, & Critchley, 2012). One possibility is that feelings of familiarity for a stimulus arise when expectations related to the degree of autonomic arousal, as marked by cardiovascular feedback or other autonomic signals, are violated given the current context. If the current experienced visceral response is an unexpected increase in autonomic arousal, it may be attributed to a feeling of familiarity. Indirect behavioral support for this interpretation comes from evidence reported in our prior study on affective priming (Duke et al., 2014). As mentioned, in that study, we found that participants are more likely to endorse faces as familiar when they are preceded by the masked presentation of happy as compared to neutral faces. Critically, this effect was only present in individuals who showed no awareness of the nature of primes presented, as probed with a subsequent prime discrimination task. In other words, affect only influenced recognition decisions and experiences under conditions in which the affective signal could not be easily attributed to other sources. The findings of the current study can also be explained with reference to the role of expectation in attribution. In the context of our experimental paradigm, the precise synchronization of stimulus presentation with the presence of increased cardiovascular feedback under systole likely produced an unexpected level of stimulus-locked autonomic arousal. Thus, participants may have misattributed this arousal to familiarity even when stimuli had never been encountered before.

Given that in everyday life individuals' encounters with objects, people, and places are not systematically tied to distinct phases within the cardiac cycle, the extent to which cardiac timing influences experiences of familiarity that occur outside of the laboratory is currently unclear. We note, however, that baroreceptors also provide afferent feedback about changes in blood pressure, which have been implicated in feelings of happiness (for review, see Kreibitz, 2010) and which may shape feelings of familiarity even when stimulus encounters are not synchronized with individual heartbeats. Moreover, visceral feedback effects on feelings of familiarity in everyday contexts could also derive from other cardiovascular sources. Unexpected stimulus-induced increases in

perceptual fluency (e.g., seeing your butcher on the bus) may trigger a more general change in autonomic arousal as part of an orienting response to expectancy violations (Ben-Shakhar, 1994; Graham & Clifton, 1966). Most relevant for the current purposes, orienting responses have been linked to a transient decrease in cardiac rate—a pattern that is thought to reflect the allocation of processing resources to salient events in the environment (Graham, 1979; Graham & Clifton, 1966; Turpin & Siddle, 1983). By this view, feelings of familiarity may also result from visceral cardiovascular changes associated with attentional orienting to an unexpected increase in processing fluency. This hypothesis provides an interesting avenue for further research on the antecedents of epistemic feelings.

Future Directions

The current findings raise interesting questions pertaining to a potential link between interindividual variation in the effects of cardiac timing on recognition-memory judgments and dispositional characteristics that have previously been shown to moderate the impact of visceral feedback in other behavioral contexts (Dunn et al., 2010; Garfinkel et al., 2013; Garfinkel et al., 2014; Pollatos, Herbert, Kaufmann, Auer, & Schandry, 2007; Werner, Peres, Duschek, & Schandry, 2010). For example, there is a growing body of research demonstrating that the behavioral influence of afferent autonomic feedback is typically more pronounced in individuals who have heightened interoceptive sensitivity, that is, a heightened ability to perceive changes in the internal milieu (see Dunn et al., 2010; Garfinkel et al., 2013; Werner et al., 2010). A recent study has even linked differences in interoceptive sensitivity to the influence of cardiovascular feedback on memory formation (rather than retrieval as investigated in the current study; Garfinkel et al., 2013). Differences in state and trait anxiety have been shown to moderate the influence of visceral feedback on behavior in ways similar to interoceptive sensitivity (Garfinkel et al., 2014; see also Pollatos et al., 2007). These considerations point to the possibility that the cardiac-timing effects we observed on recognition memory judgments could also depend on an individual's ability to perceive pertinent autonomic feedback signals. Another potentially important variable to consider is gender. There is some recent evidence that cardiovascular parameters related to baroreflex functioning differ between males and females (see Fisher, Kim, Hartwich, & Fadel, 2012, for a review). Future work that includes assessment of interoceptive sensitivity (see Kleckner, Wormwood, Simmons, Barrett, & Quigley, 2015; Schandry, 1981; Whitehead, Drescher, Heiman, & Blackwell, 1977), measurement of state/trait anxiety (Spielberger, 1983), and experimentation with gender-balanced samples promises to shed further light on factors that constrain the influence of visceral autonomic feedback on memory judgments and experiences revealed in the present study.

Conclusions

The present findings have important implications for our understanding of the nature of epistemic feelings. In particular, our findings resonate with theoretical frameworks developed in cognitive psychology that emphasize the contribution of subjective feelings and experience in guiding cognitive judgments (Koriat, 2000; Moulin & Souchay, 2014; Schwarz, 2012; Tulving, 1985;

Whittlesea, 1997). The importance of subjective experience for understanding mnemonic processing was championed by Tulving (1985), who argued that recognition memory decisions can be associated with distinct phenomenological experiences (i.e., “remembering” and “knowing”) of functional relevance that can be tapped by asking participants to report their subjective experience. The current findings build on this critical distinction and provide a novel link between epistemic feelings of familiarity and the biological processes that are known to shape feeling states in other contexts. Put another way, they suggest that epistemic feelings are similar to feelings of emotion in that they draw on a common source—that is, cardiovascular feedback from the autonomic nervous system. An important goal for future research is to determine whether other epistemic feelings, such as feelings of knowing, tip-of-the-tongue states, and déjà vu experiences (see Moulin & Souchay, 2014, for a review) are also shaped by this type of visceral feedback. At a broader level, our interpretation of epistemic feelings aligns with “constructivist” views of the mind that emphasize the importance of inferential processes to the molding of subjective experience (Barrett, 2006; Jacoby et al., 1989; James, 1894; Russell, 2003; Whittlesea, 1997). In accordance with these views, we suggest that visceral feedback may be one of many cues that can be utilized in the service of recognition-memory decisions and that shape corresponding experiences.

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