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Attention and Learning through the Eyes of the Emotional Brain

Attention and Learning through the Eyes of the Emotional Brain

by Manuel Oliva

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Thesis for the degree of Doctor of Philosophy
Thesis advisors: Prof. Christian Balkenius, Prof. Annika Wallin & Prof. Halszka Jarodzka
Faculty opponent: Prof. Daniel Richardson

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Attention and Learning through the Eyes of the Emotional Brain

Abstract

The present thesis consists of four articles that address cognitive-emotional interactions as measured through eye movements and pupil dilation.

Social facilitation-inhibition is an effect that describes changes in performance (enhancement or impairment) when individuals complete tasks in social presence compared to when they perform the same tasks in solitary conditions. Along this line, Paper I and II focus on the effect of social presence in low and high level tasks, such as eye movements and learning, respectively. These are the first evidence showing that social presence influences the attentional control of eye movements.

The locus coeruleus is a brain structure that is active during arousal and stress, as well as during cognitive and attentional processes. In addition, this structure is almost the sole network mediating pupil dilation in conditions of constant luminance. Therefore, the activity of the locus coeruleus can be indirectly traced through changes in pupil size. In Paper III we investigated the role of the locus coeruleus, as measured through fluctuations in pupil size, during the process of emotion recognition. The results of this paper indicated that pupil dilation reveals the time course of decision making on emotional tasks. In Paper IV, the role of the locus coeruleus was investigated in the context of selective attention. The results revealed that pupil size predicts the efficiency of selective attention in conditions of low perceptual load (i.e., tasks few stimuli and/or simple stimuli) but not in conditions of high perceptual load (i.e., higher number of stimuli and/or more complex stimuli).

Finally, since no single theory has emerged that can account for social facilitation-inhibition, I argue in the introduction of the thesis that the locus coeruleus may be involved in mediating cognitive-emotional functions, including social facilitation-inhibition.

Key words

visual selective attention, social effects, emotion recognition, locus coeruleus

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A doctoral thesis at a university in Sweden takes either the form of a single, cohesive research study (monograph) or a summary of research papers (compilation thesis), which the doctoral student has written alone or together with one or several other author(s).

In the latter case the thesis consists of two parts. An introductory text puts the research work into context and summarizes the main points of the papers. Then, the research publications themselves are reproduced, together with a description of the individual contributions of the authors. The research papers may either have been already published or are manuscripts at various stages (in press, submitted, or in draft).

Cover illustration front: Micrograph of the locus coeruleus, which means 'blue spot'. (Credits: Wikipedia).

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Dedicated to my family
Helena, Elvira & Francisco

Contents

List of publications

This thesis is based on the following publications, referred to by their Roman numerals:

I **Influence of coactors on saccadic and manual responses**

M. Oliva, D.C. Niehorster, H. Jarodzka & K. Holmqvist
i-Perception, Volume: 8, issue: 1

II **Groups do it better? Social influences on computer-based learning**

M. Oliva & H. Jarodzka
Under Review in Computers & Education

III **Pupil dilation reflects the time course of emotion recognition in human vocalizations**

M. Oliva & A. Anikin
Under Review in Scientific Reports

IV **Pupil size and search efficiency in low and high perceptual load**

M. Oliva
Submitted to Cognitive, Affective, & Behavioral Neuroscience

All papers are reproduced with permission of their respective publishers.

Other contributions by the author not included in this thesis:

The social brain goes to school: Eye movements, instructional design and the classroom effect

M. Oliva, D.C. Niehorster, A. Wallin, C. Balkenius, K. Holmqvist & H. Jarodzka
Special Interest Group Meeting of EARLI SIG 6 2016

The presence of others: exploring the effects of a social context on eye movements

M. Oliva, D.C. Niehorster, H.Jarodzka, & K. Holmqvist
Abstracts of the 18th European Conference on Eye Movements 2015

Influence of co-learners sheer presence on multimedia learning performance

M. Oliva, D.C. Niehorster, A. Wallin , K. Holmqvist & H.Jarodzka
The Scandinavian Workshop on Applied Eye Tracking 2016

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Popular summary

This thesis is comprised of four articles that investigate social effects, learning, emotion recognition and visual selective attention.

In the first two articles I investigate the effect of social presence on the preparation of eye movements and learning, respectively. When we compete or collaborate with others on a certain task, it might seem evident that our performance may change compared to if we perform such tasks alone, in solitary. However, social psychology research has shown that even the mere presence of another person can influence our behavior and attention, even when we are not directly interacting with the other people present. That is, just the presence of others in the environment may have a huge impact in our actions. An example many people may relate to are open-office spaces — where many employees perform individual tasks but share the same space with others — versus closed-office spaces, where employees also perform individual but are alone in the room. In fact, previous research showed that the mere presence of a person can influence our behavior in different and apparently contradictory ways. Sometimes social presence makes us perform better compared to when we are alone, whereas for other tasks our performance may decrease under social presence. Although different models have been proposed to explain these effects, the underlying causes are still unknown. Eye movements are tightly controlled by attention and executive functions and I therefore used them as a way to understand the effect of social presence on such underlying processes. Secondly, the effects of social-facilitation on educational settings (like schools and universities) are not extensively researched. The second study shed more light on how social presence influences learning compared to when we study alone.

In the third article of the thesis I study emotion recognition as a cognitive ability, as well as how the time course of emotion recognition can be traced through changes in pupil size. Pupil size can vary as a function of cognitive and emotional factors. Therefore, I used pupil fluctuations to study emotional and cognitive components during emotion recognition. Normally cognition and emotion are studied as separate and independent entities that do not interact with each other that much. This view is currently changing and this article contributes to show that the interrelation between cognition and emotion is tighter than previously thought. In fact, the results of this study indicate that the time course of decisions during emotion recognition can be traced through pupil dilation.

In the fourth article I investigate visual selective attention and how this process can be studied through fluctuations in pupil size. This study is the first to show that selective attention might be mediated by activity in a small brain structure called the locus coeruleus. This structure releases norepinephrine, a neuromodulator commonly related with stress responses. This study shows that the locus coeruleus, as measured by pupil dilation, mediates attention when the amount of total visual information of the task is low (small and/or simple stimuli), in which case the visual system can perform a parallel search for information across all the visual field. In contrast, when visual information load of the task is high, not all perceptual information is processed at once and the locus coeruleus seems not to mediate attention performance. These findings establish a connection between current models of selective attention and locus coeruleus-norepinephrine physiological observations.

The experiments presented here test different cognitive and attentional capacities. However, I propose that these systems may be influenced by a common processing network in a way that renders them more interconnected than what they originally seem. This hypothesis is further developed in one of the chapters.

Part I

Attention and Learning through the Eyes of the Emotional Brain

1 Introduction

This thesis is based on four different publications. The first two papers study how social presence influences low level behavior such as eye movements (saccades) and high level processes such as learning, compared to when participants complete the same task in isolation (alone, in solitary). The third study investigates the process of emotion recognition from non-verbal human vocalizations, as measured through fluctuations in pupil size. These three studies were conducted in the 'Digital Classroom' a novel research facility at Lund University Humanities Laboratory that allows to perform eye-tracking over multiple participants at the same time. Finally the fourth paper investigates the efficiency of selective attention, also as measured through changes in pupil size.

As I argue in this thesis, I believe that all these seemingly different processes analyzed in the four papers are linked by the action of a small brain structure called locus coeruleus. The locus coeruleus was recently associated with processes that range from attention, arousal, cognition and, importantly, pupil dilation. Therefore, I first review and discuss these findings, which should help the reader understand the scope of the papers.

Paper III explores cognitive-emotional interactions in the decoding of emotional signals. Cognitive and emotional processes were usually studied as separate entities. However, current views propose integrative accounts between networks that were traditionally considered either cognitive (e.g., prefrontal cortex) or emotional (e.g., amygdala). These cognitive-emotional interactions seem to be crucial for both emotional and cognitive processing, as it seems that affective networks play important roles in cognition and cognitive areas play an important roles in emotion processing. Along this line, the results of Paper III indicate that the locus coeruleus may constitute a hub in the brain associating emotional and cognitive inputs.

The locus coeruleus is also involved in the regulation of attention. Paper IV explores this hypothesis and shows that activity in the locus coeruleus can be used to predict attentional efficiency in visual tasks.

When it comes to social facilitation-inhibition, the most influential theories that explain social effects, in particular social facilitation-inhibition, state that emotional arousal and attention play a key role in mediating these effects. Social facilitation-inhibition refers to the fact that sometimes we perform better at certain tasks when we do them in social presence (e.g., in front of an audience, or even with just others present). On the contrary, social presence sometimes impairs our performance in other task compared to when we do them in solitary.

Although social effects are widely described in the literature, there is no unifying theory of social facilitation-inhibition. As it turns, converging results show that many of the behavioral manifestations of arousal in mammals are mediated by the locus coeruleus. This includes processes such as decision making, attention and behavioral states. As such social facilitation-inhibition may be defined as a cognitive-emotional effect of social presence. Thus, at the end of the thesis I argue why social psychology should focus on the effects of locus coeruleus when addressing social influence effects.

2 Summary of the research papers

This section provides a more extensive summary of the papers included in this thesis. For further details, the original papers are included in Part II.

2.1 Paper I: Influence of coactors on saccadic and manual responses

In this study, two experiments were conducted to investigate the effects of co-action on eye movements (saccades) and manual responses. All participants completed the study individually, however they were randomly assigned to take the experiments either in an alone, solitary condition or in a group of other co-actors who performed the same tasks at the same time. In Experiment 1, participants completed a pro- and antisaccade task where they were required to make saccades towards (prosaccades) or away from (antisaccades) a peripheral visual stimulus. The sudden onset of a visual target triggers the visual grasp reflex, which tends to make observers look towards the target. As such, prosaccades are highly stereotyped responses and participants usually perform them very efficiently in this task. In contrast, antisaccades require first inhibiting this stereotyped response in order to later look towards the opposite direction. Therefore, correct antisaccade performance requires good attentional and cognitive functions. Indeed, this task is currently used for the study and diagnosis of attention deficit disorders, schizophrenia and prefrontal cortex functions. In Experiment 2, participants performed a visual discrimination task that required both making a saccade towards a peripheral stimulus and then making a manual response in reaction to the stimulus's orientation.

This study is the first in effectively showing the effects of social presence on eye movement control. The main results of this paper show that performance of stereotyped saccadic responses are not affected by social presence. In contrast, the preparation of cognitively controlled saccades is delayed by the presence of coactors. In particular, antisaccades – but not prosaccades – were influenced by the type of social context. Additionally, the number of coactors present in the group had a moderating effect on both saccadic and manual responses, where the more participants present, the larger the influence of the group. There are two main theories explaining social facilitation-inhibition but none of them is fully supported. While one of them associates arousal and stress as the underlying mechanisms mediating social facilitation-inhibition effects, the other one proposes that these are mediated by attentional mechanisms. The results of this study adds more evidence in support for the attentional view of social influences.

2.2 Paper II: Groups do it better? Social influences on computer-based learning

As in the first study, the second one addresses social effects as well, however now in the context on a high level cognitive function such as learning. This study investigates whether the presence of other students influences individual learning outcomes compared to when students perform alone (in solitary conditions). This experiment was conducted in the 'Digital Classroom' a research setting at Lund University Humanities Laboratory. This research setting was originally designed to resemble a classroom-like environment in which each student works on computers equipped with a non-invasive eyetracker.

In these experiments the influence of the social context is assessed within two multimedia learning tasks. That is, participants have to learn from learning material that contains texts and illustrations. Participants completed the experiment either alone or in the presence of other students who each conducted the same experiment individually. Previous social studies in learning focused on cooperation and competition settings, where students need to cooperate together in order to accomplish the learning task. These have shown that cooperation can enhance learning. However, cooperation can also lead to 'social loafing' effects, in which some students may pay less effort that when they work alone. The research question of the present study is different, though. Here we study the effect of the presence of other co-actors that do not cooperate nor compete with each other. This study indicates that the presence of other students can enhance learning performances. Participants in the group condition obtained higher transfer scores in both learning tasks, whereas retention performance improved only in one task. Furthermore, the analysis showed that the number of learners in the group (the group size) may moderate the effect of social presence. The study shows that social presence can significantly impact learning performances, even when working individually on computer-based tasks.

2.3 Paper III: Pupil dilation reflects the time course of emotion recognition in human vocalizations

This study investigates the relationship between pupil dilation and the process of emotion recognition. More specifically, we investigate task-evoked pupil responses of participants while they decide about the emotional states of speakers producing emotional vocalizations (e.g., laughter).

It is described that emotional signals usually cause an increase in pupil size, and this effect has been largely attributed to autonomic arousal prompted by the stimuli. Additionally, recent studies have linked changes in pupil size with decision making and perceptual processing during perceptual tasks that do not involve emotional stimuli. Therefore, in this study we investigate the relationship between pupil size fluctuations and the process of decision making during emotion recognition. For this purpose, participants were asked to hear human nonverbal vocalizations (e.g., laughter, crying) and indicate the emotional state of the speakers as soon as they had identified it. The results show that during emotion recognition, the time course of pupil response is driven by the decision-making process. In particular, peak pupil dilation betrayed the time when participants selected the emotional state of the speaker. In addition, pupil response revealed properties of the decisions, such as the perceived emotional valence and the confidence of the participants in the assessment. Under constant luminance conditions the pupil size varies almost exclusively because of norepinephrine (NE) release from the locus coeruleus (LC). Therefore, the results of this study reveal an important role of the LC-NE system during both emotional and cognitive decision making. This indicates that this region may be a hub integrating brain networks involved in cognitive-emotional processing.

2.4 Paper IV: Pupil size and search efficiency in low and high perceptual load

This article studies visual attention and how performance in visual search is predicted by pupil size. As in Paper III, here I use pupil size as proxy of locus coeruleus-norepinephrine (LC-NE) activity, a system associated with cognitive modulation. In particular, this study addresses visual attention in conditions of high and low perceptual load. A task with high perceptual load is defined as a task that contains a high number of stimuli or, alternatively, stimuli that are difficult to process. In contrast, low perceptual load describes when the task is composed by fewer stimuli that are simple to process. There are different theories that try to explain selective attention. The perceptual-load hypothesis is probably the most discussed attentional theory these days. As its name suggests, it argues that attention mechanisms are highly dependent on the perceptual load of the task. In brief, it proposes that high perceptual load presents observers with more information than they can process at any one time. In such cases, information is believed to be perceptually filtered so that only a subgroup of stimuli are fully processed. In contrast, low perceptual load allows observers to process information in parallel across all stimuli. More about these theories is described in the body of this thesis.

This study assesses the influence of LC-NE activity (as measured through pupil size) as predictor of visual search efficiency in conditions of low and high perceptual load. For this purpose, participants were asked to search for a target in search arrays with high and low perceptual load. The results show that pupil baseline size, measured during one second prior to the trial onset, significantly predicts the upcoming search efficiency only in low perceptual load, when all visual information is processed in parallel. In addition, the results show that pupil dilation and its time course predict response times in both perceptual load conditions. Thus, this study is the first to relate visual search efficiency with LC-NE function. Because this relationship is present only in low perceptual load, the results suggest that the degree with which LC-NE influences attentional performance is related to the perceptual load of the task at hand. This suggests the existence of different attentional mechanisms, one in which LC-NE activity predicts task performance, and another one where attention mechanisms seem independent of LC-NE. Finally, these results are in line with the perceptual load hypothesis of selective attention, which proposes the occurrence of different attentional mechanisms as a function of perceptual load.

Chapter 1

A selective review of selective attention

The world is full of shapes, colors, sensations, smells and sounds. There is an enormous amount of information surrounding us and yet – no matter how hard we try – we can only process a limited amount of all this sensory information at any one time.

This is the result of our own processing limitations, which manifest in our everyday lives in different ways. An example of this might be a person out on town, suddenly walking straight into a light pole, because he or she was too busy texting on the phone. Contrary to what potential bystanders might think about you, the scientific term for this is 'inattentional blindness', which occurs when we fail to notice something that is right in front of us, because we were focused on something else.

The example above also exemplifies the strong connection that attention has with consciousness. Our awareness of the world; what we see, hear and feel, not only depends on the available information out there, but also upon which aspects of this we decide to attend. Therefore, the concept of selective attention denotes those mechanisms that cause our experience to be influenced by a specific set of elements rather than another.

The process of selecting what we want to attend to sometimes depends on volitional, active mechanisms (i.e. top-down control). For instance, when we are looking for our keys, we would start by looking in places where we think they are more likely to be. In addition, selection mechanisms are also determined by the nature of each of our senses. In vision, selection is partly determined by visual acuity. Objects projected into the fovea receive better neural representations than those in parafoveal areas, just because of a differential somatosensory mapping. If our point of interest is not in the center of our visual field we will tend to shift our gaze towards it. Otherwise, if our gaze is not in the right position at the right moment, we might miss relevant information not because of volitional, top-down mechanisms but just because of a passive, physical limitation given that we were simply not able to adequately perceive such information.

Finally, even if our gaze was oriented towards the proper location of information, there are additional factors that can limit selection. If you look at a word in this text you will probably recognize and decode its meaning very quickly. However, it is not possible to just look at this page and interpret all its content at once. There is just too much perceptual information and such perceptual overload leads to a passive gauze of information.

Research in selective attention has focused on the 'locus' selective attention, or in other words, the moment throughout the perceptual process when information is selected or neglected, which determines what information access awareness.

The next sections provide an overview of the main models of selective attention. The sections follow a chronological structure, however the intention is not to provide an exhaustive review of theories but rather to explain which accounts have influenced the development of the studies presented here.

1 Early selection accounts

Imagine that you are at a lively Swedish 'fika', where people are talking about many different topics at the same time. You may be particularly keen on just one of these talks and therefore you try to focus solely on this conversation of interest. The problem is that in such a chatty environment, we need to pick out only the voices that are currently relevant to us.

This may seem like a rather simple task, we can do it naturally, without using much mental effort. However, it is not a really trivial task: constantly, our ears receive sounds of irrelevant words from other conversations that could interfere with the decoding of the attended message if they were not filtered out.

The problem presented above was actually addressed early in selective attention research and was coined the 'cocktail party' effect (Cherry, 1953). This effect led to the development of an influential paradigm in auditory selective attention, namely 'dichotic listening', which involved 'selective shadowing' tasks. The generic form of these experiments consists of simultaneously presenting the listeners with two different messages, often by means of headphones playing one message to each ear.

Participants are instructed to monitor only one of the messages, usually a speech, while ignoring the remaining one. In early experiments, participants were required to repeat aloud, or to "shadow", one of the messages. Other variations of this task required participants to monitor one of the messages without the need for verbalization, which taxes executive functions.

These studies investigated two aspects of selective attention efficiency. Firstly, researchers were interested in measuring how well individuals can extract information from the attended message. Secondly, researchers investigated how much information from the rejected message we are still able to process. These early studies conclusively showed that physical differences between relevant and irrelevant stimuli, for instance having messages spoken by very different voices, is a key factor for effective attentional selection.

Additionally, these studies showed that listeners were largely unaware of the unattended information, even failing to notice strong salient characteristics of the messages such as frequent word repetitions, changes in language and sentences played backwards (Broadbent, 1958; Moray, 1959). The general conclusion derived from the first attentional studies, in particular those using the shadowing paradigm, consistently showed that we are pretty effective at selecting the message of interest while at the same time neglecting the remaining information. This robust empirical data led to the development of the first model of selective attention.

2 Broadbent's filter model of attention

In 1958, Broadbent was the first to propose a model of selective attention capable of explaining shadowing effects. The model proposed two processing stages. It assumed that when different stimuli reach the senses, their basic physical features such as the pitch of a sound or the color of a visual stimulus, are first processed and extracted in parallel across all stimuli. This stage does not depend on attentional mediation; it proceeds in an automatic fashion and the information is temporally stored, according the the original model, in the 'S-system', from where it can be recalled for behavioral purposes. Nowadays, this system would probably be referred to as short-term, working memory.

In a second stage, the stimuli are analyzed further, in order to extract meaning and semantic, conceptual information. According to Broadbent, this is performed by the 'P-system', which has limited processing capacity and therefore works serially. The time it takes to process each stimulus depends on the amount of information that the stimulus conveys. As the analysis of a stimulus is completed a new one is allowed to enter.

In order to work properly, the P-system requires the early filtering of perceptual information so as to reduce load on it. This selection takes place based on the features extracted and stored in the S-system. In that way, the filter blocks irrelevant streams of information and allows only those stimuli that contain features of interest to pass. As a consequence, only a limited amount of information can be identified at any one time and used for behavioral purposes.

In a practical example, if we were looking for a blue jacket in the living room of our home, all blue objects would probably grab our attention first. It is possible that we'd first look towards an irrelevant blue object, but after identifying that it is not the jacket, we'd continue by checking the next blue object.

Distinctively, Broadbent's model proposes that selection occurs at an 'early' perceptual stage, before actual stimulus identification. This model can explain general shadowing effects very well by proposing that the unattended message is filtered out based on its physical properties so that only the message of interest is processed for meaning.

Early research in selective attention focused primarily on the auditory modality, however, there were some examples in vision where early selection accounts may apply. For instance, Sperling (1960) showed that when an array of many letters is displayed briefly, individuals cannot report them all. However, we become very good at reporting selected letters when a subset of letters of the array is cued. Another familiar example is happening as you read this thesis. As we read, we select and extract the meaning of the current line of a text, while at the same time we are nearly unaware of the content of the above and below rows (Willows and MacKinnon, 1973); and such information almost never interferes with our understanding of the relevant line.

Broadbent's filter model is one of the most influential models in selective attention and has implications even in current discussions about attention mechanisms. For example, the filter theory implies that attention cannot be divided between two or more stimuli because the P-system cannot perform in parallel. Any resemblance to divided attention in the performance of concurrent tasks is achieved by switching between them back and forth.

All in all, the filter account was the first formalization of a plausible attentional model, which influences even current views of attention. However, researchers quickly found conditions in which this model failed to explain selection. This led to modifications to the model, some proposed by Anne Treisman in her 'attenuation' filter account (Treisman, 1969).

3 Treisman's attenuation model

A strict interpretation of the filter model implies that unattended stimuli, filtered early in perception, should receive no processing for meaning. This was in line with early research in dichotic listening. However, researches quickly found exceptions that challenge the concept of an absolute filter. One interesting example showed that when the name of the listener is contained in the rejected ear, it still shifts attention towards the unattended message (Moray, 1959), indicating that not all information is fully filtered out. There are plenty of other examples were focusing attention does not completely prevent the processing of the

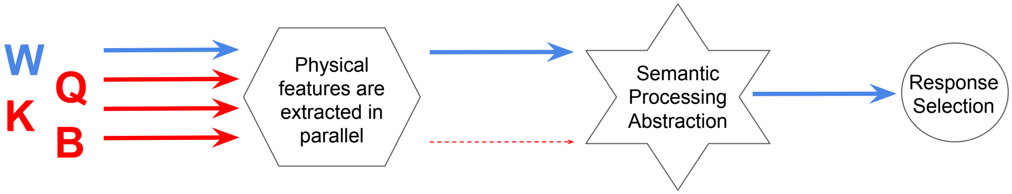

Figure 1.1: Treisman's attenuation model of selective attention. This model is based on Broadbent's Filter model and it proposes that simple stimuli properties such as physical characteristics (e.g., color, pitch) are extracted in parallel across all stimuli. In a second stage more complex properties (e.g., meaning) are extracted. This second stage is assumed to have limited capacity, so that it could not process all incoming information at once. A selective attenuation filter protects this processing system from overload, attenuating irrelevant stimuli and passing stimuli that contain features of interest.

unattended stimuli, which indicates that at least some of these stimuli are fully processed.

In an attempt to accommodate the filter theory to the new evidence, Treisman (1969) proposed a simple modification that specifically pointed to the way the filter worked. She proposed that the filter 'attenuates' the unattended stimuli rather than completely blocking them. In addition, as seen in Figure 1.1, according to this model unattended stimuli could still reach late processing stages, which would explain why listeners are sometimes aware of particular parts of the unattended message.

4 Late selection accounts

Early work in the 1950s addressed selective attention within the auditory modality because, unlike vision, audition does not require orientation movements (e.g., head and eye movements) towards the stimulus of interests as in visual attention. However, from the 1960s onwards most work focused on new visual paradigms, which changed the views on selection accounts at the time.

A classic example of visual experiments that did not follow the predictions of early selection models come from the flanker effect (Eriksen and Eriksen, 1974). In the prototypical form of this task, participants have to report the appearance of one of two possible targets (e.g., 'N' or 'X'). In addition, two more letters appear flanking the central target letters. Eriksen and Eriksen (1974) showed that when the flanker is the alternative target option (e.g., if 'X' is the target and 'N' appears as a flanker), participants' response time is slowed down compared to when the flanker is a non-target letter (e.g., 'R'). Another influential paradigm that influenced attentional models is the Stroop interference effect. In this task, a colored word naming either its own color or a different one is presented on a screen and participants are required to respond according to the coloring of the word. For example, the word 'blue' can be displayed in yellow and participants have to respond only to the color of the word. As in the flanker task, an incompatibility between the word and its color causes an increase in errors and response times.

Following predictions from the filter or attenuation model, one would expect that it should be possible to simultaneously attend to the central stimulus while ignoring flanker stimuli. In the end, this task is not very different from dichotic listening experiments, where participants had to monitor one message and ignore another one. An early perceptual filtering of the distractor would mean that only one is further processed for meaning. If this happened, there should be no competition between the identified stimuli. However, a failure to successfully filter out a competing stimulus indicates that both are actually processed for meaning and identified.

Therefore similar deficiencies of the filter model that motivated Treisman to modify to the filter model led Deutsch and Deutsch (1963) to propose a 'late' account of selective attention, which proposes that selection occurs late in processing

According to this model, all concurrent stimuli are processed for meaning in parallel and without filtering. This includes all relevant and irrelevant information. The selection of information thus occurs late in the course of information processing and after perception of all stimuli. The bottleneck in this model has to do with what information enters to awareness and response selection as perceptual information is accumulated. Given that we perceive all stimuli, this bottleneck prevents the initiation of more than one response at a time. Instead, it selects the response that best matches the requirements of the current situation. A schematic description of this model can be seen in Figure 1.2.

This model differs from early models in the way it accounts for divided attention. As mentioned above, early selection presupposes that true divided attention is not possible because only one stream of information is allowed to receive further processing at a time. In contrast, late accounts assume that all stimuli are fully perceived, which implies that divided attention should be possible.

Going back to the flanker and Stroop examples, this account assumes that both distractors and targets are equally identified, which leads to a competition for a behavioral response. Therefore, late selection accounts explain why the presence of a competing distractor (i.e., the other target alternative) causes slower responses and increases error rates. Paradoxically, late accounts fail to explain shadowing effects, for which early accounts seem to fit better. According to late accounts there should be no such thing as an 'unattended' message, all stimuli are processed for meaning, which is contradictory to findings that listeners are often little aware of the content of the rejected message.

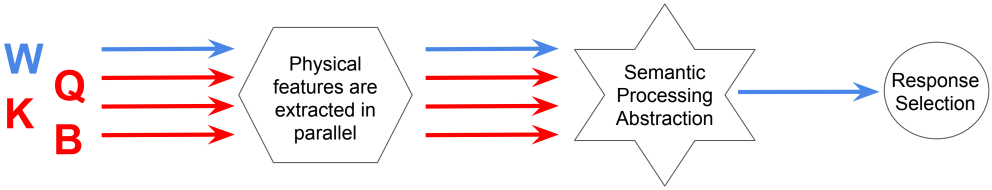

Figure 1.2: Late selection model of selective attention. Late accounts propose that all stimuli receive full perceptual analysis but only one is responded to. Selection has to do with which stimulus is used to provide a relevant behavioral response.

In sum, while early accounts excel at explaining attentional selection under certain conditions, such as shadowing effects, late accounts seem to be a better model in other types of situations, like flanker experiments.

The early vs. late discussion kept researchers busy during many years in order to find a resolution to it (Kahneman and Treisman, 1984; Treisman and Gelade, 1980). In fact, there seems to be a general difference between these experiments that may unify early and late models. Late selection usually occurs when the main task involves high 'perceptual load', that is, when the task comprises many stimuli or when these are difficult to process. Early selection, on the other hand, seems to explain well task that involve low perceptual load, that it, task composed by fewer stimuli or stimuli that are easy to process. This observation was made by Lavie and Tsal (1994), who proposed the perceptual-load hypothesis reviewed in the next section.

5 Perceptual-load hypothesis

In a review of selective attention, Lavie and Tsal (1994) noted that results supporting late or early selection views had typically been reported in tasks with different 'perceptual load'. Perceptual load is operationalized as the amount of perceptual demands of a task. A task with low perceptual load has, for example, a small number of simple stimuli, while a high perceptual load task has a higher number of stimuli and/or more complex ones. Lavie and Tsal (1994) noted that low perceptual load usually favored late selection mechanisms. An example of low perceptual load tasks are flanker experiments that use only one target and one distractor.

In a series of experiments Lavie (1995) and Lavie and Cox (1997) measured distractor interference in conditions of high and low perceptual load. They found that the presence of a distractor harmed selective performance exclusively in conditions of low perceptual

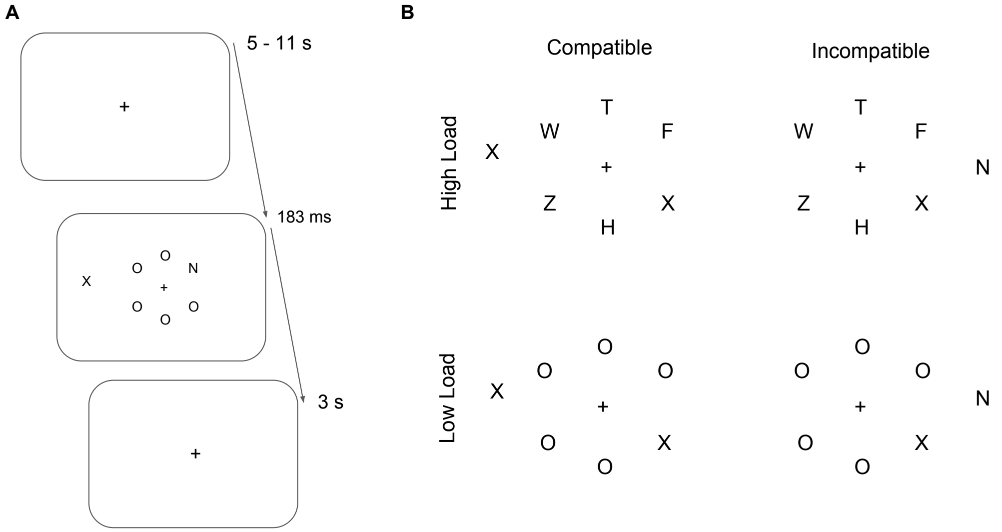

Figure 1.3: Example of a task used used in Paper IV for the study of selective attention under low and high perceptual load. (A) A circular array of letters is displayed for less than 200 ms to preclude the use of eye movements. Participants are ask to report the target letter (X or N) that appears within the central array while ignoring a peripheral distractor presented outside the search array. (B) The perceptual load of the task is manipulated by embedding the target between letters that are either more similar (high load) or less similar (low load) than the target letters.

load. In contrast, when the perceptual load of the task was increased, the same distractor caused little or no effect compared to when no distractor is present. This effect was studied with a task that could be thought as an adaptation of the flanker task. As observed in Figure 1.3, an array of letters is displayed for a brief amount of time and participants have to respond which of the two possible target letters is presented within the search array. In addition, a distractor appears outside this array, which participants are instructed to ignore. The distractor can be either 'compatible' (same as target) or 'incompatible' (the alternative target). The perceptual load is manipulated by changing the similarity of the letters in the search array (see Figure 1.3).

The perceptual load hypothesis proposes a resolution between late and early accounts and combines both models. As in traditional late selection (Deutsch and Deutsch, 1963), the perceptual-load hypothesis assumes that perceptual processing proceeds in an automatic fashion; all perceptual information is fully processed with no early filtering of information that would preclude full perceptual analysis. But as in classic early selection (e.g. Broadbent, 1958), this account assumes that perceptual capacity is limited. Therefore, this implies that the extent to which the target task exhaust available resources will determine whether or not there will be spare capacity to process irrelevant information. With low perceptual load, spare capacity will 'spill over' to irrelevant information, including distractors. But if the target task is higher in load, this may consume the available capacity, leaving less resources for the processing of irrelevant information.

6 Dilution hypothesis

Some researchers have recently challenged the perceptual-load hypothesis. They propose that the effect of perceptual load is actually attributed to the 'dilution' of the distractor within the stimuli present in the main task (Benoni and Tsal, 2013; Tsal and Benoni, 2010; Murphy et al., 2016). In low load there are fewer stimuli present than in high load and therefore the presence of a distractor may be more salient in low load than when the array contains high number of stimuli (high load). Importantly, although dilution accounts differ from the load-hypothesis in the way high load would reduce distractor interference in high load, both agree with the fact that late selection mechanisms are involved under low perceptual load.

7 Implications for my thesis

Selective attention determines which information will receive awareness. Although research is still focused on understanding such mechanisms, one of the last accepted views, the perceptual-load theory, seems to provide a plausible link between early and late mechanisms. According to this view, experimental conditions that promote late selection mechanisms imply that all information will receive full perceptual analysis. Selection then requires active cognitive engagement to decide which parts of all this information is behaviorally relevant. In contrast, if perceptual load is high, it seems that selection occurs under a more passive filtering mechanism, where we are just not able to cope with all stimuli and, as a consequence, not all sensory information is perceived. This other mechanism seems not to rely so heavily on cognitive mediation as late selection does. Therefore, early and late models have different predictions about the cognitive demands involved in attention. I explored this hypothesis in Paper IV, where I used pupil size as a marker of cognitive processing to predict the efficiency of visual search in conditions of low and high perceptual load. Because pupil size under isoluminant conditions reflects cognitive and affective states (Sara and Bouret, 2012; Joshi et al., 2016), I predicted that pupil size should mostly reflect attentional performance only in conditions that depend on cognitive mediation, or in other words, that use late selection mechanisms. In fact, the results of Paper IV validated this hypothesis, revealing different mechanisms involved in the processing of high and low perceptual load information. In particular, pupil size preceding each trial predicted the upcoming trial attentional performance only in conditions of low perceptual load. These results are the first to link pupil size with attentional performance in high and low perceptual load, and the first to link attentional performance with pupil size as an indirect measure of behavioral state. This hypothesis is further developed in the next sections and should become clearer for the reader.

Pupil size fluctuations under isoluminance conditions have been linked with noradrenergic (Joshi et al., 2016) and cholinergic (Lovett-Barron et al., 2017; Reimer et al., 2016) neuromodulation in the brain. Therefore, recent studies have been exploiting pupil measures as a proxy of neuromodulatory activity in the brain while participants engage in affective and cognitive tasks (see Papers III and IV). Section 2 reviews this evidence and provides a more physiological perspective of attention. In addition, I propose why pupil size may be a good substrate for the study of selective attention (and social effects, which are addressed in Section 3).

Chapter 2

Locus coeruleus, pupil size and the control of behavior

The pupil of the eye fluctuates in size almost on a continuous basis. Most of the time these fluctuations have to do with the light reflex where the pupil regulates the amount of light reaching the fovea, the part of the retina that offers the highest visual acuity. However, researcher have found that pupil size also varies as a function of working memory load. In an old experiment, Kahneman and Beatty (1966) asked participants to memorize series of digits which they had to report back briefly after presentation. Kahneman observed that the larger the series of digits participants had to report, the larger their pupils increased in size.

More recent studies (Aston-Jones et al., 1994; Usher, 1999) using single neuron recordings in monkeys showed that under constant luminance conditions, pupil size correlated with activity in the locus coeruleus (LC). The LC is almost the sole source of norepinephrine (NE) in the mammalian brain. It consists of only a few thousand neurons (approximately 16000 per hemisphere in humans), but despite its small size, it sends inputs to several brain regions such as all cortical areas, the thalamic nuclei, hippocampus, and basal lateral amygdala. In turn, the LC receives inputs from the orbitofrontal cortex (OFC), the anterior cyngulate cortex (ACC), amygdala, the vagus nerve and the nucleus paragigantocellularis. These afferent and efferent inputs of the LC places this tiny structure in a key connectivity position, suggesting that it may act as a hub relating different brain networks.

Two of the papers included in the present thesis deal with pupil size measures as a way to investigate attentional and cognitive-affective processes. Therefore, in this chapter we explore why pupil size fluctuation may reveal important information about attentional and cognitive processing.

1 LC-NE, arousal and cognitive functions

Norepinephrine is a neuromodulator of the central nervous and its action is usually associated with arousal and stress responses. Experiments with animals that were subject to electroshocks or exposed to other types of stressors all showed increased levels of NE. In addition, long term stressful conditions increase the connectivity between LC and the amygdala, another of the structures believed to mediate stress responses (Sara and Bouret, 2012; Ramos and Arnsten, 2007).

Apart from mediating stress responses, NE has been implicated in a number of other cognitive processes. NE released by the locus coeruleus plays a key role in prefrontal cortex (PFC) function, a region tightly related to executive functions and the control of behavior (Miller and Cohen, 2001). In particular, PFC function is required for cognitively controlled behavior as opposed to more automatic, reflexive actions. There are sets of behavioral patterns that do not require high cognitive and attentional mediation in order to be performed. These can either be innate, stereotyped (hardwired) behaviors or responses that we develop through experience and learning. These sorts of behaviors usually rely on what is defined as “bottom-up” processing, that is, they are mostly determined by a mapping between the nature of the sensory stimuli and well-represented neural networks that connect these with corresponding responses. In fact, a vast percentage of our daily actions and responses consists of these stereotyped behaviors that we can deploy almost without any attentional control. Think for instance when you tie your shoes. Normally we can do this without engaging much cognitive effort. However, if you try to invert the roles of your hands, that is, to do with your right hand what your left hand would do and so on, it becomes a tremendously costly action. When the conditions afford automatic, dominant behaviors, the PFC displays low activation. On the contrary, in conditions where dominant or reflexive behavioral patterns should be inhibited in order to give place to more cognitively controlled behaviors, the PFC is highly activated. There is a growing body of evidence suggesting that one of the main roles of PFC is to inhibit or ‘cancel’ automatic behaviors so that slower, cognitively mediated responses can develop. In fact, much of these conclusions are derived from PFC lesions, which cause an increase in impulsive behavior and distractibility (Szczepanski and Knight, 2014).

Paper I

Paper I of this thesis investigates automatic and controlled eye movements (saccades) that depend on cognitive mediation, and how these are differentially affected by social presence. One marked reflexive behavior is the 'visual grasp reflex' (Hess et al., 1946; Hutton, 2008) by which we tend to automatically look and saccade towards unexpected movements or sound that occur in the environment. This study uses the antisaccade task (Antoniades et al., 2013), where participants have to inhibit the visual grasp reflex while instead making a controlled saccade towards another direction. The results of this study indicate that the mere presence of other participants slowed down cognitively controlled eye movements but did not affect those that rely more on bottom-up processes.

The PFC is subject to crucial neuromodulation. When NE (and dopamine) in the PFC of monkeys is depleted with a neurotoxin, animals become as impaired as those with PFC ablations, which exemplifies the critical role that neuromodulation plays in cortical areas (Ramos and Arnsten, 2007).

NE can have different effects on target neurons, depending on the receptors that are activated. There are four types of NE receptors in the brain and their activation is dose-dependent. Pharmacological studies show that moderate levels of NE enhance PFC function, but as arousal and NE levels increase, a different set of receptors is engaged which puts PFC functions 'off-line' and activates the amygdala, hippocampus and sensorimotor cortices, all brain networks that support more reflexive, automated behavior (Ramos and Arnsten, 2007). This may provide survival value by promoting more habitual or reflexive mechanisms that can be executed quickly during threatening conditions.

2 Simple sensorimotor decision-making

In simple sensorimotor tasks, individuals are usually required to detect and respond to the presence of a simple target within a bunch of irrelevant stimuli (think of the attentional tasks in Chapter 1, for example). The problem is that the perceptual information we get from the world usually arrives to the senses as imperfect, noisy sensory information. Therefore, if we were to respond according to every incomplete piece of sensory input we received, our behavior would be erratic and imprecise. A more plausible decision mechanism would be to provide some period of time in which perceptual information is accumulated and integrated over time. As sufficient information — or evidence — in support of a perceptual alternative is obtained, a behavioral response can then be initiated.

This basic decision mechanism depicted above is the basis of several influential decision models, such as the diffusion drift models (Ratcliff and McKoon, 2008; Ratcliff and Van Dongen, 2011) and the LATER model (Carpenter and Reddi, 2000; Carpenter, 1981), used in Paper I.

These models are not only theoretical propositions but can also accurately explain response time and error distributions in different decision tasks (Noorani, 2014; Gold and Shadlen, 2007). For instance, response times can be faster if evidence accumulation occurs at a faster rate, in which case a decision threshold would be reached sooner. In contrast, it is also possible to achieve faster response times by lowering the decision threshold, in which case there may be more response errors due to insufficient evidence integration. Finally, empirical findings from neurophysiological experiments have supported these models after revealing correlates of neural activity that increase with sensory input until an activity threshold is reached, after which a behavioral response is triggered (Purcell et al., 2012; Schall and Bichot, 1998).

Paper 1

In Paper I, we used a decision model (LATER) to compare saccadic response time distributions of participants performing in solitary or under social presence. The results indicated that the slower response times in the social condition was due to an increase in decision threshold. This indicates that participants prolonged the period of information accumulation before initiating saccadic movements.

3 The LC-NE and the regulation of behavior

LC activity was usually associated with the general modulation of arousal effects, but recent accounts propose more specific roles of this system in the regulation of sensory processing. Experiments studying visual signal detection in monkeys showed that when a target embedded within a stream of irrelevant stimuli is devised, it triggers a strong phasic LC-NE response (Foote et al., 1980; Aston-Jones et al., 1994). Such phasic responses are traceable through the task-evoked pupil response (Joshi et al., 2016; Privitera et al., 2010).

Apart from phasic responses, the LC displays a constant level of tonic or basal neural activity at any given time. The tonic activity varies, for instance, following sleep-wake cycles and arousal states. Basal and phasic LC activity have received a lot of attention in the last years because different studies showed that they correlate with neural and behavioral responsivity

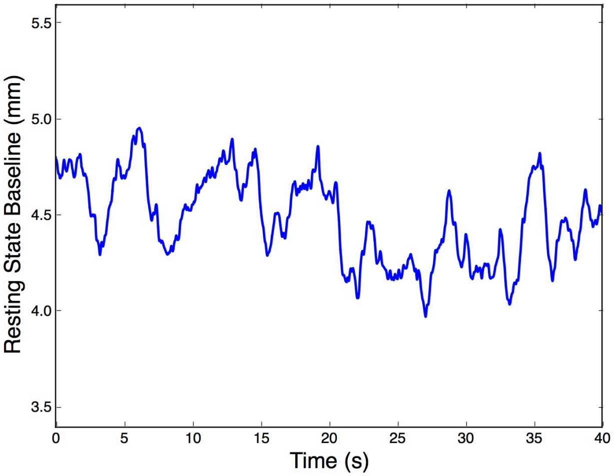

Figure 2.1: Pupil fluctuation during passive fixation and constant luminance conditions show spontaneous fluctuations that corresponds with LC tonic activity (Joshi et al., 2016). The LC tonic activity was linked to neural responsivity to sensory stimuli.

to sensory stimulation (Gilzenrat et al., 2010; Aston-Jones et al., 1994; Usher, 1999). Early studies showed that NE modulates neural activity in cortical circuits, where it increases the ratio of task-evoked activity to spontaneous activity (Foote et al., 1975). At the neuronal level, the effect of NE is to augment evoked responses while reducing irrelevant or spontaneous activity of the same neuron. The effects of NE were also studied in behavioral task in monkeys performing go/no-go tasks where the animals had to release a lever every time a 'go' signal appeared within a rapid visual stimuli presentation (in order to obtain juice as reward). These experiments revealed that periods of moderate tonic LC-NE activity levels were associated with large phasic LC responses and enhanced target detection performance. In contrast, high tonic levels (high responsivity) were associated with small phasic bursts and increased false positive responses to non-target stimuli. Very low levels of tonic activity, instead, are associated with low performance due to drowsiness. A perceptive reader may quickly link the effects of the LC-NE system with the Yerkes-Dodson inverted-U relationship between arousal and performance. Theories of social presence effects have given arousal and its effect a key role in mediating for instance social facilitation-inhibition. More about this and the Yerkes-Dodson relationship is further examined in the next chapter.

The observation that strong phasic responses correlate with good target detection performance (as in the go/no-go example) has led researchers to propose that phasic responses have an important role in simple sensorymotor decision-like processes, for example in deciding whether a stimulus is a target or not (Einhäuser et al., 2010; Aston-Jones et al., 1994; Gilzenrat et al., 2010). In line with this view, marked phasic responses would facilitate behavioral responses to the outcome of decision processes, filtering responses to irrelevant stimuli (note similarities with attentional models which propose the filtering of irrelevant information, see Chapter 1.4). The way LC-NE influences neural processing is not fully understood, however, many studies suggest that 'gain' modulation may be a plausible mechanism.

4 Gain modulation

The main mechanism of NE action in the brain is 'neuromodulation'. That is, rather than it triggering excitatory or inhibitory responses as traditional neurotransmitters, NE role is mostly confined to modulate the effect produced by other neurotransmitters such as glutamate (excitation) and GABA (inhibition) (Mather et al., 2015). The exact mechanisms by which NE elicits its effect are yet not fully understood. However, different studies converge on the fact that NE action mechanism is to increase 'gain' in its target neural networks, usually cortical areas (Aston-Jones and Cohen, 2005; Usher, 1999). The basic idea behind gain modulation is that NE enhances the activation of neural inputs that already present high activation, but also enhances inhibition of networks that are less active. The outcome of this modulation is an increase in contrast between weak and strong neural inputs, which improves the signal-to-noise ratio of neural inputs (Waterhouse and Woodward, 1980; Usher, 1999). Recent studies support this hypothesis, for instance findings from Devilbiss and Waterhouse (2011) agree with such view and also conclude that LC influences signal processing by optimizing behaviorally relevant neural computations through changes in gain. Also, imaging studies (Warren et al., 2016) using fMRI to assess the effect of NE on perception found that increases in gain enhance the precision of mental representations of visual stimuli as measured by 'angular dispersion', a metric that estimates the quality of neural representations.

Computationally, the effects of gain are said to influence the activation function of single neurons or networks. The activation determines the relationship between the input (x) of the system and its output, usually represented by a logistic function of the form,

$$f_G(x) = \frac{1}{1 + e^{Gx+B}} \tag{2.1}$$

In a single neuron, the output represents the firing rate of the unit given a certain level of sensory input, for instance. The enhancing effects of NE on responsivity can be modeled as a change in the shape of the activation function. This can be performed by increasing the value of the gain parameter (G). The response function includes a bias (B), which is observed in the response function of actual neurons (Servan-Schreiber et al., 1990).

All in all, one of the main roles of the locus coeruleus–norepinephrine system consist of enhancing, through gain modulation, neural representations that are behaviorally relevant, while at the same time reducing spontaneous activity. LC neurons can be phasically activated in response to task-relevant stimuli so that to temporally enhance representations that are most relevant for task performance. Strong neural representations, that it, those that are already somewhat active (because of either bottom-up and/or top-down signals) are enhanced by norepinephrine, whereas weak neural representations are more inhibited. More of the effects of NE and gain are discussed in Section 9.

5 LC-NE pupil dilation

Many studies addressing LC-NE function pointed correlations between neural activity in this area and pupil dilation, reflecting both tonic and phasic activity (Rajkowski, 1993; Aston-Jones et al., 1994; Usher, 1999). Recently, a dedicated experiment corroborated that pupil fluctuations under isoluminant conditions are largely attributed to LC activity and activity from its proximal areas (Joshi et al., 2016). Although the majority of evidence underlines a noradrenergic influence in pupil dilation, there is also supportive results showing cholinergic modulation (Reimer et al., 2016).

As such, these findings open possibilities for new studies, which could use pupil measures instead of more complicated intracellular recordings of LC activity. Some studies have recently investigated decision-making and perceptual processes through task-evoked pupil dilations, and their findings are addressed in the next sections.

6 LC-NE system and perceptual decisions

Recent studies have linked pupil dilation to perception in simple choice tasks. Einhäuser et al. (2010) studied pupil dilation during bistable perception. This study used a Necker cube as stimulus. The Necker cube (see Figure 2.2) can be perceived in tow possible ways (it has two possible percepts). In this study, participants had to look at a Necker cube for a certain amount of time and press the space bar key every time they experienced a shift in the perceptual interpretation of the figure. The results showed that every perceptual shift was followed by a phasic pupil response. Moreover, the amplitude this pupil response was proportional to the time participants preserved such perceptual interpretation until the next perceptual shift. In other words, phasic pupil responses predicted the temporal stability of percepts. Therefore, researcher associated phasic responses with a post-decisional role, in which, LC-NE responses consolidated perceptual interpretations.

The idea of a post-decisional role of LC-NE function was challenged soon after. Instead of using a clear target as in the studies reported before, de Gee et al. (2014) used a grating signal superimposed onto dynamic noise. In this experiment, a bunch of dots moved in a

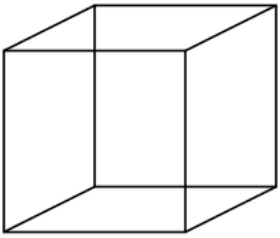

Figure 2.2: The Necker cube can be perceived in two possible ways. The perceptual experience of looking at this figure will usually alternate between the two possible percepts.

random walk pattern on top of a grating signal so to add noise to the detection of the target. As a result, this task requires the gradual accumulation of noisy perceptual information so to decide about the presence or absence of the target stimulus. In contrast to previous findings that propose a post-decisional role of LC-NE (Einhäuser et al., 2008; Aston-Jones and Cohen, 2005), this study showed that the largest component of pupil dilation was detected during the formation of decisions — and not at the end. Therefore, the authors of this study stressed an important intra-decisional role of LC-NE.

Paper III

In Paper III we investigated task-evoked pupil responses while participants formed decisions about the nature of emotional human vocalizations. Vocalizations are relatively complex perceptual stimuli, in the sense that its recognition requires accumulation of perceptual information in order to be successfully identified.

The results showed that pupil dilation increased in a sustained fashion during the decision process, supporting an intra-decisional role of LC-NE during decision-making. By time-locking the pupil response to the moment of the decisions, we showed that pupil responses aligned with the time course of the emotional recognition process and revealed the timing of the participants' choices. In addition, pupil response amplitude revealed both the confidence with which participants decoded the emotional vocalizations and the perceived emotional valence intensity of the sounds.

In contrast to purely visual tasks, emotional recognition involves additional brain networks such as those engaged in auditory processing and those activated during emotion processing, e.g. the amygdala.

7 LC-NE in attention

Brain areas thought to be involved in attentional processing (e.g., parietal cortex, superior colliculus) as well as motor areas (e.g., motor cortex) receive a particularly dense LC-NE innervation (Foote & Morrison 1987). In fact, some attentional phenomena are believed to be connected to the working mechanisms of LC. An example of these is the 'attentional blink' effect, observed in Figure 2.3. This paradigm consist of asking participants to observe a 'rapid stimuli visual presentation', in which stimuli appear one after another in intervals of $\sim$100 ms. Individuals are asked to report the two targets (let's say T1 and T2) that appear within the stream of irrelevant stimuli (see Figure 2.3). For instance, numbers can be used as irrelevant stimuli and letters as targets. When T1 and T2 are placed right after each other (lag 1) there is a small facilitation in the probabilities of reporting T2, that is, T1 slightly facilitates T2 identification (this is called lag 1 sparing). However if T1 appears between lags 2 and 4 (lag 2 would correspond to the sequence: T1, non-target, T2), the probability of the participant reporting T2 drops dramatically (Zylberberg et al., 2012; Raymond et al., 1992). The probability of consciously detecting T2 raises back to normal levels again when T2 appears after lag 5.

This effect was coined 'attentional blink' and describes a temporal window in which we are 'attentionally blind' to sensory stimuli. It is believed the attentional blink relates to the working mechanisms of LC. When we consciously detect T1, LC triggers a phasic response in which a high percentage of all LC neurons produce action potentials. This process is accompanied by a task-evoked pupil dilation. After firing, LC cells suffer from a refractory period during which they cannot fire again because of a negative feedback caused by NE release. Even if another target is presented no phasic response would occur. This refractory period starts after 50 ms of stimulus detection and last around 450 ms. The temporal coupling between LC refractory period and the temporal window when we are attentionally blind led some to propose that LC and this mechanism explains this attentional effect (Nieuwenhuis et al., 2005; Warren et al., 2009).

Interestingly, it seems that the attentional blink effect has little to do with the stage of perception, that is, the attentional blink does not cause the suppression of either perceptual or semantic processing of the target T2 (as revealed by the presence of event related potentials, ERPs, that indicate so). In contrast, the signal corresponding to T2 is lost at the stage when it should access working memory, revealed by the absence of specific ERP components (Vogel et al., 1998). Therefore, these results suggest that we are able to process T2 for meaning and identification, but somehow the stimulus cannot be stored in working memory so to be accessed later for report.

This results bring us back to attentional models, which all have in common the existence of a processing bottleneck that limits the amount of information we can consciously perceive.

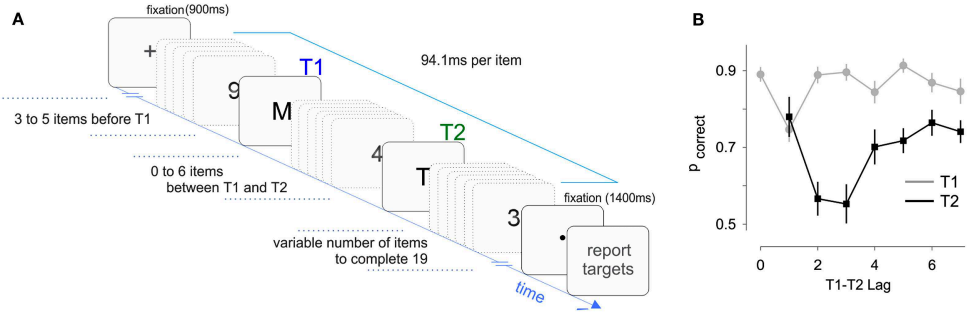

Figure 2.3: Attentional blink effect. (A) Two targets (T1 and T2) are embedded within a rapid visual stimuli presentation and participants are asked to report the targets after presentation. (B) When T2 is presented at lag 1, there is usually a slight facilitation in the probability of reporting it correctly. However, between lag 2 and 4 this probability drops significantly. Attentional performance is recovered after lag 4. The attentional blink effect coincides with the refractory period observed in LC that occurs after phasic responses. Figure extracted with permission from Zylberberg et al. (2012)

8 Lateral inhibition

Lateral inhibition is almost an ubiquitous mechanism present in different sensory systems (Amari, 1977; Olsen and Wilson, 2008), which also seems to be modulated by the LC-NE system. Lateral inhibition is the mutual inhibition of neurons or networks between each other. As described for gain, the result of mutual inhibition is to enhance the contrast between weak and strong neural inputs. When two competing neurons or networks are active, they may also exert some degree of inhibition onto each other. The amount of inhibition that a neuron can induce onto competing neurons is proportional to their own level of activity. Thus, highly active neurons will inhibit surrounding neurons more than what the less active neurons will inhibit the more active neurons. Although lateral inhibition may increase general levels of inhibitions, the result is an increase in contrast between strongly active neurons and those that are less active, which receive the strongest part of the inhibition.

Lateral inhibition is very common in sensory networks, for instance in pressure sensors in the skin. If you apply some pressure onto your skin with one finger, the area that receives the strongest inhibition will inhibit the area around the point of pressure. In this way, the brain will receive a more precise information about the exact contact location. Lateral inhibition is very common in the visual system in order to enhance contrast between sensory stimuli (Solomon et al., 1993; Blakemore et al., 1970; Mcpeek and Keller, 2014) and is also present in simple animals like insects (Montero et al., 2017; Meinhardt and Gierer, 2000), revealing that is a widespread neural mechanism.

Recent evidence also indicate that the LC-NE system may modulate the extent of lateral inhibition (Mather et al., 2016). LC–NE activity seems to activate inhibitory interneurons, in particular those (GABAergic) that are implicated in mediating lateral inhibition (Salgado et al., 2012).

9 Physiological evidence in visual selection

In this section we can resume the idea of selective attention developed in the previous chapters. The key point behind selective attention was that given our limited processing capacities, some sort of perceptual selection must occur in the course of information processing.

Researchers investigating the physiological substrate of attention have noted mechanisms by which different neural representation of sensory inputs compete with each other for cognitive resources. Along this line, Desimone and Duncan (1995) proposed that attention is the result of many neural mechanisms working to resolve competition for visual processing and control of behavior.

Desimone proposed that many neurons in visual cortex, which respond preferentially to different stimuli, are mutually inhibitory. This means that the more active a network representing a stimulus is, the more it will inhibit related networks. Desimone's interesting proposal states that our apparent attentional 'capacity limits' emerge because not all of the stimuli can receive a neuronal representation at once. Instead, these are mutually inhibitory, such that different stimuli will compete to drive the neurons and tend to produce a 'winner-takes-all' outcome. Indeed, a more recent study showed that phasic burst of LC (that induce high gain) in primary visual cortex causes weakly active neurons to be suppressed, resulting in an enhancement of strongly active neurons (Schäfer et al., 2009).

The reader may have noticed the similarities between the mechanisms mediating attention proposed by Desimone and Duncan (1995) and those recently discussed about neural gain and lateral inhibition. I therefore suggest that it is possible that the LC-NE system mediates neural gain in perceptual networks so as to sometimes increase and sometimes reduce competition between stimuli by influencing the extent of mutual inhibition. As a result, the gain of the system would mediate the range of stimuli that are able to receive cognitive representations. Low gain may allow to distribute resources over a broader range of stimuli, where inhibition between them is reduced. High gain, instead, may promote selection of a narrower range of sensory cues, where those that receive higher bottom-up and/or top-down activation will 'win' against the weaker stimuli. As a result, the LC-NE system may influence perception in a way that may become dominated by the strongest input at the expense of the weaker.

Chapter 3

Social Effects

Social presence can influence our behavior and attention probably more often and more pervasively than we are aware of. For instance, imagine that you are giving a talk at a conference or a seminar. One would probably be a little bit more alert in such a situation than if an audience wasn't there. Alternatively, imagine that you are a competitor running a race. The presence of other runners would likely set ourselves in a different mood, in which we would want to perform well in comparison to others, than if we were running alone. Evaluative and competitive social conditions may be a clear factor affecting our behavior. However, the extent to which social presence influences our behavior goes beyond these examples. Social presence influences are not restricted to the presence of an audience or other competitors, conditions which could set us in a more evaluative or competitive mood. Instead, social psychology experiments show that just the mere presence of others can make us behave significantly different than when we are alone (Richardson et al., 2012; Risko and Kingstone, 2011; Zajonc, 1965).

In this chapter, we will particularly focus on social facilitation-inhibition influences; that is, how individual performance in different tasks is enhanced or impaired by social presence compared to when individuals perform in solitary conditions.

First, I will go through some of the more influential views on social facilitation-inhibition. As for selective attention theories, there is not yet a social effect theory that can unify findings. Here I will point out some of the main theories and hypothesis, and later, I will propose why I think that neural gain and lateral inhibition may be plausible and parsimonious mechanisms for explaining social facilitation-inhibition across a wide range of tasks and animals.

1 Social facilitation-inhibition

As described above, social facilitation inhibition refers to the process in which social presence enhances or reduces a person's performance compared to when individuals complete the same task in solitary, single conditions. The first documentation of this effect was provided by Norman Triplett (1898), who observed changes in performance when athletes performed alone compared to when they performed together with other athletes at the same time. In particular, he observed that cyclists competing alone (against the clock) performed worse than those co-performing with other athletes.

Such observations led other researchers to conduct further investigations. The first results showed that social presence usually led to facilitation effects. Allport (1920) and Dashiell (1935) provided early examples of social facilitation in task such as multiplication, word associations, and simple motor responses, where in general results tended to indicate a social enhancement of performance. However, other further of findings from similar experiments showed, instead, social inhibition of performance in tasks such as problem solving, which involves coming up with elaborate responses (Allport, 1920; Dashiell, 1935; Zajonc, 1965).

The occurrence of both enhancement and impairment of performance in social presence appeared first incoherent and challenged any attempts to generalize the effects of social presence. These seemingly paradoxical findings found an explanation when Zajonc (1965) proposed his theory of social facilitation-inhibition. This account was the first to propose a framework that could account for such divergent effects on performance.

1.1 Drive theory of social effects

Zajonc's Drive theory of social facilitation-inhibition (Zajonc, 1965) argues that the mere presence of others will increase an individual's 'drive', 'activation' or arousal levels, in an automatic and unconditional fashion. In particular, Zajonc's account puts emphasis on 'audience' conditions, that is, the presence of a non-evaluative audience (i.e., other observers), and on 'co-action' conditions, in which other individuals complete the same tasks at the same time but in a non-competitive way. However, Zajonc argues that the mere presence of others is a sufficient condition for increasing drive and, as such, for social facilitation-inhibition.

Zajonc (1965) borrowed the concept of 'drive' from the Hull-Spence theory of behavior. Hull proposed a formula to explain the likelihood of making a specific behavioral response given the occurrence of a given stimulus. This formula includes the idea of drive and it looks as following: $E = H \times D \times K$ where E is the probability (and speed) of a producing a particular response in reaction to a specific stimulus, H represents the habit strength of such response (which may depend on experience and practice), D represents the amount of drive, and K represents the reward for responding. Therefore, the formula predicts that, given the occurrence of a specific stimulus, the probability of making a behavioral responses follows a multiplicative relationship between the habitual strength of such response, the animal's 'drive' to respond and the potential reward obtained given that the response is initiated. The formula includes more terms, which were left out because they are not so relevant for the present discussion. In the original formula, drive represents some biological needs, with hunger being one of the most important in animal experiments. Zajonc, instead, proposes that the idea of drive can be extended to general arousal. Because the definition of arousal is more clear than that of drive, we will just refer to this component as arousal from now on. However, note that Zajonc's theory is often referred at as 'drive' theory of social facilitation-inhibition.

According to Zajonc's theory habitual responses, defined as those responses that are easily deployed, either because they are just simple or because the individual or animal has learned it through experience, will be facilitated by general arousal, which will increase the likelihood of producing such dominant responses. In contrast, when a more elaborated response is required, that is, when the task is more complex or when the individual has not yet acquired a habitual response for it, higher arousal will still increase the likelihood of more dominant, habitual responses, which in this case will likely be incorrect, inappropriate responses. As a result higher arousal will impair performance in complex tasks. On the other hand, this also implies that reduced arousal should improve response selection when the situation requires more controlled actions from the individual.

We can go a little bit further in the analysis of habitual responses and contemplate the case in which a stimulus evokes more than just one habituated response. In the case that a stimulus evokes not a single response but a hierarchical set of possible responses, generalized arousal ('drive') will enhance differences in habit strength between them. This should increase the probability of the most dominant response within such set and decrease the probability of subordinate responses.

Zajonc's interpretation was very important when it was proposed because it allowed integration between divergent and contradictory findings, as those briefly described above. Following this account, for instance, simple motor responses should be facilitated by social presence because they are the dominant and most habitual response in such tasks. In contrast, difficult problem solving that requires coming up with novel solutions are predicted to be inhibited by social presence. Zajonc's seminal paper ends with a little piece of advice for students. He recommends to study and learn alone, and once one knows the subject, arrange evaluations in the company of other students.

Other approaches based on generalized 'drive' or arousal

According to Zajonc's view, the mere presence of other conspecifics is a sufficient condition in order to increase an individual's level of arousal. However, this view was contested by others who argued that arousal in a social context is caused by additional factors, not only mere presence.

Some of these views propose that arousal is caused by social comparison, where participants may be more concerned about how they perform in comparison to others. According to the views summarized next, arousal comes from managing social expectations, where individuals anticipate socially positive or negative consequences that increase arousal level. As such, these views argue that social effects may be influenced by learned responses from prior social experiences.

Evaluation approaches

Some researchers claim that arousal in a social context comes from preoccupations of being evaluated by another individual (Cottrell et al., 1968) or by performing so that to match a social standard level (Carver and Scheier, 1981).

As in the original Drive theory, Cottrell et al. (1968) attributed performance enhancement or inhibition to elevated levels of arousal. However, the evaluation approach underlines that the substrate of arousal does not come from mere presence of others but from the possibility of being evaluated and judged by others. Therefore, evaluation accounts predict, in contrast to the original Drive theory, that the mere presence of others who do not have the potential to evaluate our performance should not elicit any influence. In addition, this view adds that social influences may be learned and determined from prior social experiences.

Although Cottrell et al. (1968) did not differentiate between positive or negative performance evaluations, others found that upward and downward social comparisons affect the extent of social influences. Different studies show that facilitation-inhibition arises from the participants' beliefs of whether they are co-acting together with others that are better or worse than them at the respective tasks (Muller et al., 2004; Muller and Butera, 2007).

In the line of social evaluation effects, a recent paper (Belletier et al., 2015) shows that being observed by the experimenter (who could be considered an expert in the experimental task), impairs performance in tasks that require executive functions. Also, a recent imaging study found that social evaluation affects activity in attentional brain regions (Yoshie et al., 2016), which they postulate as areas mediating these effects. More about attentional effects as mediators of social effects are discussed later in this chapter.

Alertness hypothesis

Zajonc's (1980) alertness model proposes that the effect of social presence is to increase uncertainty in the environment. That is, the presence of others should set us with some degree of preparedness or alertness to respond, interact or just observe what happens with other individuals around us. This increased alertness is what causes arousal.

Monitoring hypothesis

Guerin (Guerin and Innes, 1982) borrowed the alertness idea and proposed that individuals engage in the monitoring of the social environment, especially when the situation creates uncertainty. Social situations that promote uncertainty will motivate individuals to monitor the social environment and increase generalized arousal. For instance, the presence of others that cannot be visually inspected will increase uncertainty and arousal, as will also the presence of others who are unfamiliar and hence more unpredictable to the individual.

Personality traits

A review and meta-analysis (Uziel, 2007) of social facilitation stresses on the fact that some personality traits may modulate an individual's approach to social presence and, therefore, modulate the extent of facilitation-inhibition of performance. This view focuses on individual differences and shows that individuals with more negative predispositions to social contexts may suffer from increased impairment in social situations.

Self-presentation

Bond (1982) and Guerin (2010) pointed out that the opportunity to engage in self-presentation in front of an audience is an important factor influencing performance and 'drive'. This view states that individuals try to create an impression of competence in front of others, which may increase efforts to perform better. This model, however, does not clearly explain performance impairments.

Some additional comments about these theories

Although there is evidence that evaluative conditions may increase social facilitation, many other studies show that mere presence is a sufficient condition to trigger social effects (Normand et al., 2014; Paulus, 2015; Guerin, 2010; Bond and Titus, 1983). A plausible conclusion that can be derived from such evidence is that the different approaches summarized above, instead of explaining social effects, may have more of a modulator role on social effects, where certain conditions enhance or decrease social facilitation-inhibition.

1.2 Attentional accounts of social effects

Sanders et al. (1978) proposed that the presence of other people constitute a distracting factor. The reason, they argue, as to why others are distracting are the same as those described above; for instance, it may sometimes be related to feeling more evaluated or wanting to compare oneself to a social standard. As a result, individuals will not only focus on the task at hand but some cognitive resources will also be deployed to task-irrelevant information. This attentional conflict can surely lead to an impairment of performance. But, in addition, Sanders et al. (1978) argued that such attentional conflict can increase drive (arousal) levels and lead to the typical changes in performance associated with facilitation-inhibition. Although this account could be grouped as a drive-theory, it led to the development of an attentional view of social effects, which is summarized next.

The distraction-conflict theory

The idea that social presence may cause an attentional conflict was taken by Baron (1986) and Cohen (1978), who proposed a theory of social facilitation-inhibition mediated (mostly) by attentional mechanisms instead of on the concept of 'drive'.

Baron (1986) proposed that social presence leads to cognitive and attentional overload. Given our limited attentional capacity, the occurrence of attentional overload will force individuals to attend to a narrower range of stimuli from the task at hand. That is, since some of the attentional resources are used for the monitoring of social stimuli, less resources are left available for the task at hand.

But how does this theory explain enhancement and decrements in performance in complex and simple tasks? Task complexity can be classified according to the amount of advance information required for the preparation of a relevant response. Normally, complex tasks requires integration of a wide range of stimuli. In such a case, a narrower scope of attention will have detrimental results in performance because it may cause individuals to leave important information unattended. Simple tasks, in contrast, usually require dividing attention into a smaller range of relevant stimuli than in complex tasks. In these tasks, large ranges of cue utilization provide no benefit and may even handicap performance. For instance, it is well described in educational research that adding redundant information to a learning material increases cognitive load on students and hampers learning (Mayer and Massa, 2003; Paas et al., 2010). Many stimuli may be redundant or irrelevant for solving such simple tasks. In those cases, the narrowing of attention may facilitate performance by focusing attention to only relevant stimuli while reducing potential interference coming from irrelevant stimuli. We should note again that the definition of complex and simple tasks may also relate to the prior experience of the actor with the respective tasks. A task that requires high attentional demands from a novice might be simple for an expert who may be able to divide a task into fewer chunks.

This theory of social effects has a close resemblance to attentional views of selective attention. The attentional conflict depicted here could probably be associated with the perceptual load hypothesis of selective attention (Lavie, 1995), which poses that attention to stimuli will proceed in an automatic fashion until capacity limits are reached, after which not all stimuli will be filtered early in perception. Interestingly, the distraction-conflict theory was proposed before the perceptual load hypothesis.

Finally, Baron's hypothesis equates social presence to any other kind of non-social stimuli that would create an 'attentional conflict'. Although this theory intends to explain social effects, it does not attribute social presence any other attribute than that of being a salient and distracting factor. Any other kind of distracting stimulus may cause the same pattern of performance change.

Paper I

Paper I explores the effect of attention on eye movements that depend on cognitive mediation (antisaccades) and eye movements that do not depend in high degree on attentional control (prosaccades). The antisaccade task presents participants a highly challenging attentional task. Prosaccadic eye movements are caused due to the visual grasp reflex, they are pretty reflexive responses in the sense that they require little attentional mediation. In contrast, antisaccadic eye movements may be seen as a subordinate behavior; it is a response that requires executive control to first inhibit a reflexive prosaccade response. In terms of social facilitation, prosaccades should be facilitated by social presence because they are dominant responses. In contrast, antisaccade responses should be inhibited by social presence because these responses do not come first in the repertoire of possible responses. This paper is the first evidence for social facilitation-inhibition effects on eye movements.

1.3 Some remarks

As discussed above, there is a broad number of social theories that try to account for social-facilitation effects. Some of these even stress on the effects of specific personality traits, whereas others point at self-presentation issues (the way we would like to be seen by others), as being important factors determining facilitation-inhibition. These proposals contrast with the fact that social facilitation-inhibition effects have been described across a wide range of tasks and animals, including chickens, ants and monkeys (Zajonc, 1965; Bond and Titus, 1983; Reynaud et al., 2015). Even insects such as cockroaches are influenced by the presence of other conspecifics. Zajonc et al. (1969) showed that cockroaches solve complex mazes slower when in the presence of other cockroaches (both in audience and co-action conditions) than when they are alone, but on the other hand, their performance on a simple runway task was facilitated by cockroach presence.

Therefore, a concluding remark about the hypotheses discussed in this chapter is probably that no plausible theory has emerged that can efficiently account for social facilitation-inhibition. In addition, the lack of integration between different accounts partly handicaps the value of social facilitation theory in general. After all, a distracted reader may eventually conclude that a cockroach runs faster in a maze because it wants to impress its six-legged friends.

In the next sections I will try to argue why concepts from the previous chapters may provide a more integrative view of social facilitation-inhibition effects. This view proposes that shifts in performance in social presence can be explained by simple modulation effects that are present in animals with either complex cognitive systems such as humans, or animals with simpler cognitive systems such as ants, cockroaches or even the author of this thesis himself.

2 A neural gain model of social facilitation-inhibition

I hypothesize that the simple neuromodulation that mediates neural gain and lateral inhibition may provide a broader account of social facilitation inhibition. This modulation may interconnect seemingly unrelated processes such as attention, arousal and social facilitation-inhibition.

2.1 Drive theories explained by neural gain

The basic idea mediating social facilitation according to Zajonc's generalized drive theory is that activation, drive or arousal increases the likelihood of selecting dominant responses at the expense of more elaborate, controlled behavior. This mechanism is particularly similar to that of the effects of neural gain on behavior. Let's recall that neural gain increases the contrast between strong and weak neural representations, leading to 'winner-takes-all' patterns where weaker response alternatives are more inhibited. In a similar fashion, arousal caused by certain social arrays may induce the modulation of cognitive functions as expected from that observed from the LC-NE system.

The effects of arousal on task performance were described extensively aside from social effects. For instance, Easterbrook (1959) noted that increases in arousal leads to a reduction of cue utilization, meaning that individuals tend to use a narrower range of cues in order to solve a task. Similar observations were recently made in experiments that manipulated arousal levels through other mechanisms. Since arousal is linked to motivation, Ariely et al. (2009) showed that very high monetary rewards reduce performance in tasks that involve creativity. Tasks that demand creative solutions require thinking 'outside the box'. Examples of these tasks are those that require manipulating stimuli beyond their common functional attributes, in other words, they require 'breaking' the functional fixedness of objects (Duncker, 1945; McCaffrey, 2012; Grant and Spivey, 2003) and find alternative solutions.

The effects of norepinephrine are supported by neurophysiological data. Some reviews (Sara and Bouret, 2012; Ramos and Arnsten, 2007; Arnsten and Rubia, 2012) indicate that high levels of norepinephrine promotes reflexive behavior, that is, responses that are more stereotyped and automated. This reviews underlined the joint action of the four types of norepinephrine receptors. While intermediate levels of norepinephrine release facilitate prefrontal functions (i.e., attentionally controlled behavior), high levels of norepinephrine during increased arousal seem to reduce prefrontal cortex function, allowing more habitual or reflexive mechanisms. In addition, too low levels of norepinephrine are associated with drowsiness. This relationship was reported before for the effects of arousal and is known as the Jerks-Dodson law (Figure 3.1). More evidence shows that norepinephrine mediates emotional influences on memory consolidation in the amygdala and hippocampus (McGaugh et al., 1996).

All in all, the hypothesis that social effect are mediated as part of LC-NE function provides predictions that are clearly testable. In addition, current computational models of LC-NE function based on, e.g., the models described in Chapter 2 provide a formal interpretation of the predictions derived from this system, with the possibility to predict and quantify the effects of such modulation on task performance.

2.2 Attentional view of social effects explained by neural gain

One of the main sources of support of attentional accounts of social effects comes from Stroop performance in social presence. Huguet et al. (1999) showed that social presence facilitates Stroop performance and he interpreted such results as suggesting that social presence narrows attention (or maybe improves selective attention) to the relevant features of the task. Recall that in the Stroop task the name of a color, for example 'red', may be displayed in red or in a color that is not denoted by the word (e.g., displayed in blue).

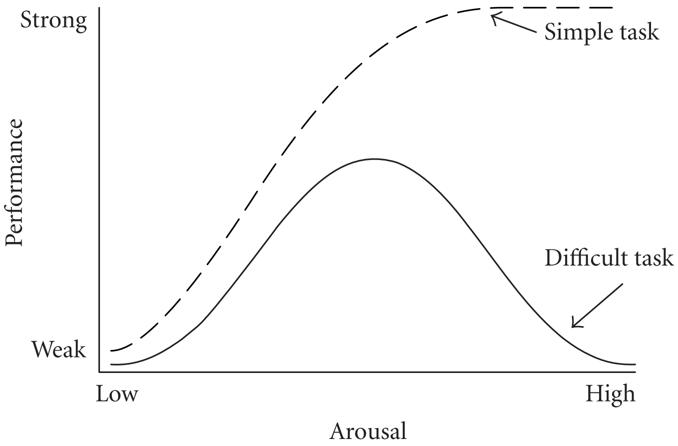

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Figure 3.1: Yerkes-Dodson relationship between arousal and task performance. A similar relationship between task performance and LC-NE activity is also reported (Aston-Jones and Cohen, 2005; Sara and Bouret, 2012; Arnsten and Rubia, 2012). Performance in simple tasks is facilitated by increased arousal/norepinephrine activity. This modulation tends to facilitate well-learned, stereotyped behavioral responses. On the other hand, the facilitation of dominant responses may impair performance in difficult tasks.

When these two do not match, naming the color of the word takes longer and is more prone to errors than when both the color and the word are congruent with each other. The distraction-conflict theory of social effects equates social presence with any other kind of non-social distractors. In this sense, some data support the paradoxical fact that, sometimes, external distractors (e.g., social presence, noise) reduce intra-task interference (e.g., word-color congruency). There are some results that support this view, for instance, previous studies showed that noise improved task-related attentional performance in the Stroop task (Hartley and Adams, 1974; O'Malley and Poplawsky, 1971; Chajut and Algom, 2003).

Another example when distraction sometimes improves performance is observed in the antisaccade task. In this task (used in Paper I), participants are asked to look towards the opposite direction of a target that appears at the periphery of the participant's visual field (i.e., if the target appears on the right side, participants have to look towards left). Although this may seem like a silly task, we normally make around 20% direction mistakes because we tend to reflexively initiate an eye movement towards the location to the target. These errors are believed to be caused by the strong visual reflex that makes us look towards things that move or pop-up in our visual field. This reflexive response requires to be inhibited if the individual wants to actually look towards the opposite side.

Regarding this task, it was shown that dual-task distraction that taxes executive function tend to reduce antisaccade performance (Roberts et al., 1994; Stuyven et al., 2000). However, another study showed that it is possible to improve performance in this task by specifically distracting participants just before the onset of the trials (Kristjánsson et al., 2001). Interestingly, the authors of that paper argue that this sort of distraction may disrupt the initiation of reflexive responses, which, in turn, would facilitate the production of alternative controlled responses. In other words, disrupting the dominant response may have the consequence of facilitating subordinate responses.

Paper I

In addition, the results of Paper I partly support an attentional view of social effects. In this study, however, social presence impaired performance in an antisaccade task. This is also the first evidence of co-action effects on eye movement control.

To wrap up this idea a bit, there is evidence that noise and distractors (social and non-social) can improve performance in the Stroop and antisaccade task. However, instead of this being a facilitation of top-down controlled behavior, it may be caused by an impairment of stereotyped responses that indirectly allows the execution of subordinate behaviors. From my point of view, the effects of social presence on attention should be investigated more carefully. In particular, the task presented in Paper IV would be a suitable task to assess attentional effects of social presence, in particular because of the following reasons. First, it uses a task that is widely studied in selective attention research. Secondly, it was adapted in order to be conducted under isoluminant conditions, allowing for the study of pupil fluctuations as indicator of LC-NE function.

Attention and norepinephrine

Attention holds a tight link with arousal. Kahneman (1973) proposed, based on pupil dilation data, that attentional overload triggers transient increases in effort and arousal. Kahneman argued that the effects of distraction may be resisted at the cost of the manifestations of increased arousal. The idea that mental effort correlates with arousal is supported by studies showing that metal effort causes an increase in pupil size (Kahneman and Beatty, 1966; Porter et al., 2007; Takeuchi et al., 2011; Bijleveld et al., 2009).

From this point of view, it can also be derived that an external source of distraction such as social presence may as well affect arousal levels as demands on attention also increase (Sanders et al., 1978).

Thus, an attentional account of social effects may also be explained through the mediation of neural gain and lateral inhibition as a source for interpreting behavioral and attentional shifts in social settings. As discussed in Chapter 2, Desimone and Duncan (1995) showed that different stimuli compete with each other for neural representations. This means that neural sensory representations inhibits each other in a process that is analogous to lateral inhibition. If the competition between sensory representations is modulated so that those stimuli that receive stronger top-down (or bottom-up) signals become more active in relation to weaker representations, it would be possible to reduce interference from irrelevant sensory stimuli that may interfere with the selection of a response. Additional supportive evidence coming from imaging studies show that norepinephrine has a facilitatory effect in enhancing the precision of sensory neural representations (Warren et al., 2016).

In addition and as discussed in chapter 2, evidence shows that tonic levels of LC-NE activity mediate the ability to resist distraction in monkeys (Aston-Jones et al., 1994; Aston-Jones and Cohen, 2005) and humans (Gilzenrat et al., 2010). Paper IV presented in this thesis also reports a strong relationship between visual attentional performance and pupil size, where the pupil size preceding each trial predicted the subsequent trial response time.

Paper IV

Paper IV investigates the relationship between pupil size and efficiency in a selective attention task. Although this task was not used to assess the effect of social presence, the results reveal mediation of LC-NE on visual selection performance. Because the attentional mediation of social effects requires deeper understanding, the task presented in Paper IV provides a task that is ready to be tested in social contexts: it provides pupil data and robust predictions about selective attention and, therefore, any influence caused by social presence should be detected with this task.

In summary, the effects of neural gain and lateral inhibition may provide a more actualized and accurate description of the effects that social presence may have on individuals. As we discuss below, analogous neuromodulatory mechanisms can mediate similar effects in simple organisms.

Neural gain across a wide range of animals

A neuromodulatory view of social effects provides an easier explanation of effects across animals with very different cognitive systems. Firstly, insects present analogous norepinephrine neuromodulators that mediate arousal responses (Farooqui, 2007). Secondly, lateral inhibition is described in insect sensory neural mechanisms (Montero et al., 2017; Laurent, 1999) and the idea of gain control through reciprocal inhibition is also widely studied in insect models (Baca et al., 2008).

Pupil dilation and social presence

A benefit of the neural gain theory of social effects is that it provides clear predictions about how attentional and behavioral responses should be affected by social presence. In addition, norepinephrine activity levels are easily measurable through changes in pupil size (Joshi et al., 2016). This provides the unparalleled opportunity to assess the effects of mere presence on indirect physiological variables of LC-NE activity. If the predictions of the neural gain account of social effects are correct, these modulations should be revealed through fluctuations in pupil size as a proxy of LC-NE function. Therefore, pupil dilation should constitute a key measure of the extent of social facilitation-inhibition, where the effects of the social context should be traceable through fluctuations in pupil size.

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Part II

Scientific publications

Author contributions

My contribution to the present papers involved in all cases experimental design planning, programming and setting up eye-tracking experiments, conducting the experiments, data collection, eye-tracking data processing, statistical analyses and manuscript writing.

Paper I

Article

i-PERCEPTION

Influence of Coactors on Saccadic and Manual Responses

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Abstract

Two experiments were conducted to investigate the effects of coaction on saccadic and manual responses. Participants performed the experiments either in a solitary condition or in a group of coactors who performed the same tasks at the same time. In Experiment 1, participants completed a pro- and antisaccade task where they were required to make saccades towards (prosaccades) or away (antisaccades) from a peripheral visual stimulus. In Experiment 2, participants performed a visual discrimination task that required both making a saccade towards a peripheral stimulus and making a manual response in reaction to the stimulus's orientation. The results showed that performance of stimulus-driven responses was independent of the social context, while volitionally controlled responses were delayed by the presence of coactors. These findings are in line with studies assessing the effect of attentional load on saccadic control during dual-task paradigms. In particular, antisaccades – but not prosaccades – were influenced by the type of social context. Additionally, the number of coactors present in the group had a moderating effect on both saccadic and manual responses. The results support an attentional view of social influences.

Keywords

Attention, cognition, divided attention/resource competition, endogenous/exogenous, eye movements, social cognition

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Introduction

Imagine writing an exam in a large hall where row after row of other students take the same test. You hardly look at each other, let alone talk, but you are likely to think about their progress compared to your own, and you experience how their presence affects your thoughts and actions. One can think of many situations where our behaviour is influenced by the type of social context we are in. Indeed, research has shown that even the mere presence of another person can affect our attention and actions (Richardson et al., 2012; Zajonc, 1965). A meta-analysis of 241 studies found that the presence of others improves the speed at which simple tasks are completed but decreases the speed for complex tasks (Bond & Titus, 1983). Although these social effects have been thoroughly studied, their causes are still debated (Guerin, 2010). Explanations of how social presence affects task performance often refer to attentional and cognitive processes, so in this study we set out to test two major social theories with eye movement paradigms that specifically reveal attentional and cognitive processes.

The simple presence of other individuals can lead to either an increase or decrease in task performance of participants compared to when they complete the same tasks but in solitary conditions. This is referred to as the social facilitation–inhibition effect. Two major theories have been proposed to explain its causes. First, Zajonc's (1965) Activation Theory postulates that the presence of other people increases the individual's arousal and drive, and that this, in turn, shifts the likelihood towards displaying automatic, well-learned responses rather than cognitively controlled responses. In consequence, social presence improves performance on simple tasks requiring automatic responses but reduces performance on tasks that require cognitively mediated responses.

Secondly, Baron (1986) and Sanders, Baron, and Moore (1978) provide an alternative theory for social facilitation and inhibition, named the distraction-conflict theory. This theory is based on the view that attention is a limited resource (Broadbent, 1971; Cohen & Spacapan, 1978; Kahneman, 1973) and holds that the presence of other people competes with the task at hand for attentional resources. If individuals additionally attend to the social environment instead of exclusively attending to the task, attentional resources will be redirected away from the task. This competition for attentional resources has been shown to lead to a focusing of attention on information central to the task (Cohen & Spacapan, 1978; Easterbrook, 1959; Geen, 1976). On the one hand, such a narrowing of attention can improve performance by increasing the focus on task-relevant information and limiting the interference from distractors. For example, social presence reduced interference in a Stroop task (Huguet, Galvaing, Monteil, & Dumas, 1999) and an illusory conjunction task (Muller, Atzeni, & Butera, 2004). On the other hand, the distraction-conflict theory predicts that attentional focusing will impair performance on tasks that require the use of a larger range of information (Baron, 1986). In this study, we test these predictions specifically for visual attention and the extent of the functional visual field.

Previous Studies of Eye Movements Under Social Presence

In recent years, eye movement research has increasingly been conducted in social settings such as supermarkets (Gidlöf, Wallin, Dewhurst, & Holmqvist, 2013), cars (Recarte & Nunes, 2003) and psychiatric clinics (Hutton & Ettinger, 2006; Munoz, Armstrong, Hampton, & Moore, 2003), where other individuals might be present besides the participant or patient. As such, researchers have recently begun to investigate how social presence influences eye movements. For instance, in situations where there is potential for social interaction, attention to social stimuli changes compared to solitary experimental conditions (e.g., Foulsham, Walker, & Kingstone, 2011). The possibility of interaction also changes the extent to which participants follow each other's gaze to stimuli in the environment (Gallup, Chong, Kacelnik, Krebs, & Couzin, 2014). More importantly, a recent study (Richardson et al., 2012) found that even the mere presence of another person can influence attention allocation. Richardson et al. (2012) seated pairs of participants facing in opposite directions and showed them sets of pictures with positive and negative emotional valence. Although the individuals did not interact with each other, the belief that they were looking at the same stimuli at the same time shifted participants' gazes towards the more negatively valenced pictures, compared to when they believed that their partner was engaged in a different task.

Previous research on eye movements and social presence has focused on social attention and the perceptual function of exchanging and sharing information with others. In contrast, our aim is to explore whether the presence of others affects the attentional state of individuals in a way that can be traced through eye movement paradigms.

Saccades and Attention

The presence of others has been shown to influence individuals' attention and action (Baron, 1986; Zajonc, 1965). Therefore, a possible avenue for the study of social presence might be provided by eye movements, which are intimately related to attentional processes (Hoffman & Subramaniam, 1995; Walker, Deubel, Schneider, & Findlay, 1997). In particular, saccades are rapid eye movements that bring the fovea onto a target of interest. This process can be driven by stimuli in the environment, in which case the saccade responds to an automatic, bottom-up saccadic program, or the saccade can be regulated in a topdown fashion, such that volitional control is used to attend to targets that are in line with task-relevant goals of the observer (Buschman & Miller, 2007; Theeuwes, 2010; Trappenberg, Dorris, Munoz, & Klein, 2001). The balance between controlled and automatic behaviour is regulated by cortical areas that have the ability to inhibit automatic responses in favour of controlled responses. Neurophysiological experiments have shown that the superior colliculus mediates bottom-up, reflexive saccadic eye movements (Braun, Weber, Mergner, & Schulte-Mönting, 1992; Schiller, Sandell, & Maunsell, 1987), whereas cortical areas such as the frontal eye fields and the dorsolateral prefrontal cortex are involved in higher levels of oculomotor control (see Munoz & Everling, 2004, and Hutton & Ettinger, 2006, for reviews), including the inhibition of the superior colliculus and its automatic saccades (e.g., see review by Johnston & Everling, 2008) in favour of taskrelevant volitional saccades.

The *antisaccade* task (Hallett, 1978) was designed to investigate the mechanisms responsible for generating automatic versus controlled eye movements. In this task, the participant either makes a prosaccade towards a sudden-onset target, or an antisaccade away from it. While prosaccades are automatic eye movements (Roberts, Hager, & Heron, 1994), antisaccades require cognitive mediation, first to inhibit the automatic prosaccade, and second to plan and generate a saccade in the direction opposite to the target (Everling & Fischer, 1998; Olk & Kingstone, 2003). Patients with frontal lobe lesions or prefrontal dysfunction usually show poor antisaccade performance, with prolonged response latencies and increased direction errors, because they lack the ability to suppress the automatic saccade towards the target (Guitton, Buchtel, & Douglas, 1985; Hutton & Ettinger, 2006; Jantz, Watanabe, Everling, & Munoz, 2013; Johnston & Everling, 2008; Munoz et al., 2003). However, poor executive control in the antisaccade task is not exclusively observed in patients. Dual-task manipulations that increase attentional load also impair the performance of antisaccades, but not prosaccades, in healthy participants to levels similar to those of prefrontal patients (Baddeley, 1992; Roberts et al., 1994; Stuyven, Van der Goten, Vandierendonck, Claeys, & Crevits, 2000). Such studies suggest that increased attentional load interferes with the normal executive control that cortical areas deploy over the superior colliculus. This leads us to think that in a social context the competition for attentional resources may elicit results similar to those previously found for dual-task manipulations on saccadic control.

Programming saccades requires the processing of visual information to reach a decision as to where to move the eye (Hanes & Schall, 1996; Paré & Hanes, 2003). Neurophysiological studies, indeed, demonstrate that neural activity in the frontal eye fields and superior colliculus accumulates linearly after target appearance, and it is only when the activity reaches a critical level that a saccade is launched (Gold & Shadlen, 2000; Hanes & Schall, 1996; Paré & Hanes, 2003). Therefore, current models for saccade generation suggest that the distributions of saccade reaction times can be studied as the result of such neural decision mechanisms (Noorani, 2014; Schall & Bichot, 1998; Schall & Hanes, 1998). The LATER model ('Linear Approach to Threshold with Ergodic Rate'; see Carpenter, 1981; Carpenter & Williams, 1995; Reddi & Carpenter, 2000) characterizes saccade latencies in terms of the rate at which information is accumulated and approaches a threshold for deciding to launch a saccade. Little is known about how social presence influences saccade programming. Here we analyse whether the change in speed for launching a saccade between social conditions is due to a shift in the decision threshold or due to a change in the rate of information accumulation.

The Present Study

In this study, we test the effect of the presence of coactors on automatic and controlled behaviour and discuss our findings in the light of social facilitation–inhibition theories. We use paradigms that target attention and oculomotor control as seen in eye movements. For this purpose, we compared the performance of participants in two conditions, one in which the participant conducted the tasks in the presence of others who did the same task at the same time (group condition), and another condition in which participants conducted the task alone (solitary condition).

In the first experiment, participants performed an antisaccade task and we measured how pro- and antisaccades were affected by the presence of coactors. Based on the distraction-conflict theory and studies that showed the effects of attentional load on saccade generation (Stuyven et al., 2000), we expected the following: if the presence of others competes for attentional resources, antisaccade latencies should increase in the group condition whereas the rate of direction errors will not be affected by social presence. Prosaccade performance, on the other hand, will not be affected in the group condition compared to the solitary condition, as these are automated responses.

In contrast, activation theory has different predictions: because the presence of others increases the individual's arousal, the activation theory predicts a shift towards automatic behaviour in the group condition. Therefore, in the group condition, the automatic prosaccade response is expected to become easier (latencies decrease), while the controlled antisaccade response becomes more effortful (latencies increase). For the same reason, we expect increased antisaccade direction error in the group condition, due to an increased difficulty in suppressing the automatic prosaccades.

In the second experiment, we extend our findings using a different task. Specifically, participants completed a choice reaction time task in which they had to make a saccade to a peripheral target and give a manual response to indicate the target orientation. This task involves an automatic saccade to the target, similar to the prosaccades in Experiment 1, but it additionally features a manual response, which constitutes a controlled response. Again, activation theory predicts facilitation in automatic saccades (lower latencies), but impairment in the manual responses.

Additionally, we looked at the moderating role of group size on coaction effects. We expect that bigger group sizes would increase participants' awareness of the presence of others, which would enlarge social influence effects (see, e.g., Latane & Zipf, 1981).

Experiment 1

In order to assess whether the presence of coactors affects the voluntary control of eye movements, we employed the antisaccade task described above. We compared performance in a solitary condition with that in a group condition. In the group condition, participants performed independently of each other but in a group setting, and all were aware that they conducted the same task at the same time.

Methods

Participants. Fifty-two participants (Mean age = 26.2, standard deviation (SD) = 5.4; 18 women) were recruited via the Internet, gave informed consent and received a movie ticket for participation. All had normal or corrected-to-normal vision. Group sizes varied from two to eight participants per recording session and averaged 4.0 participants (SD = 1.8). Participants who came to the group conditions were not told during recruitment that the experiment was conducted in groups to avoid selection effects. Four participants with an antisaccade error rate higher than 50% were excluded from the analysis; eight other participants were excluded due to excessive data loss (see 'Data analysis'). In total, 20 participants were included in each condition.

Design. The experiment used a 2 × 2 mixed design in which social condition (group or solitary) was varied between subjects (20 participants for each condition) and type of saccadic reaction (pro- or antisaccade) was varied within subjects.

Stimuli and material. Following the recommendations by Antoniades et al. (2013), the antisaccade task consisted of 120 antisaccade trials presented in three blocks of 40 trials with optional breaks in between, and two blocks of 40 prosaccades each at the beginning and end of the task. Participants had to look at a central cross presented for a random interval between 833 ms and 2333 ms. The stimulus was presented randomly either to the left or right of the central fixation point, 9.9 cm away from the centre, which corresponds to 9.4° at a distance of 65 cm. The target was a white dot with a diameter of 0.53° (5 mm).

Apparatus. The experiment was presented on 22" monitor screens (Dell P2210, 1680 × 1050 at 60 Hz). Each of the computers was equipped with a RED-m remote eyetracker (SensoMotoric Instruments, Teltow, Germany) that recorded eye movements at a sampling rate of 120 Hz with a visual-angle accuracy of 0.5°, as reported by the manufacturer. Participants were calibrated in order to get an accuracy below 0.5°. When it was not achieved after three calibration attempts, validation results below 1° were accepted. The average validation accuracy was 0.70° ± 0.14°. The room in which the experiment was conducted consisted of 25 computers, each with one eye tracker.

Procedure. Participants received a short verbal introduction to the task during which they were informed that all people in the room would perform the same task. Participants were asked to work in silence and to avoid causing disturbance. Further detailed task instructions were presented on the screen, to ensure that participants understood the task, and to prevent participants from asking questions that would disturb others. In the group condition, participants sat adjacent to each other in a row of eight computers, separated from each other by approximately 100 cm. Participants sat at adjacent computers, regardless of the size of the group, to avoid differences in participant spacing due to differences in session sizes. Once all participants were successfully calibrated, participants were instructed to start the antisaccade task at the same time. The solitary participant recordings were performed in the same research facility. In both social conditions, the experimenter was in the room in a covert position that was not visible to the participants.

Data analysis. The start of the saccadic movements was detected by a custom version of an adaptive velocity-threshold-based event-detection algorithm (Nyström & Holmqvist, 2010). The saccade reaction time was defined as the time between the appearance of the stimulus and the start of the saccade away from the fixation point. Saccade onsets were determined by fitting a line to the part of the saccade where acceleration was positive and computing where this line intersected the abscissa. Trials where the starting fixation deviated more than 3° from the central fixation cross or where data samples were missing during the saccade were excluded. Saccades with a latency of less than 50 ms were considered anticipatory responses and excluded. Participants for whom less than 70% of the trials had a usable saccade under these criteria were excluded. Saccadic direction errors were coded as wrong when the first saccade after target presentation was in the wrong direction, that is, towards the stimulus during antisaccades.

As the distribution of latencies in response tasks is known to exhibit significant skew with a longer tail than a standard normal distribution (Carpenter & Williams, 1995; Reddi & Carpenter, 2000), the reciprocal of the saccadic reaction time, which does follow a Gaussian distribution (Noorani, 2014; Reddi, Asrress, & Carpenter, 2003) was used for all analyses. Participants are sometimes seen to make so-called 'early responses', saccades with extremely short latencies that do not belong to the main distribution of latencies (Carpenter & Williams, 1995; Munoz & Everling, 2004). Early responses were identified by fitting Carpenter's LATER model (see 'Computational modelling') to the saccadic latency data. Specifically, when the reciprocals of the saccadic latencies are plotted on probit axes, the main population of responses falls along a straight line. The early responses are apparent from an inflection of the line at the early end of the distribution of latencies. Following Carpenter (Carpenter & Williams, 1995), per participant, the saccadic latencies in this space were fitted with two straight lines, one line with an unconstrained slope and intercept and one line whose intercept was fixed to the median of the latency distribution. Any saccades with latencies shorter than the intersection point of these two fitted lines were considered early and removed from further analysis. As identified by the LATER fit, there were scarce occurrences of early responses per participant in both the group (1.32 ± 0.30) and solitary conditions (1.07 ± 0.33).

We report t values and 95% confidence intervals for parameter estimates b arrived at through linear mixed effects modelling (Pinheiro & Bates, 2000) using R 3.0.1 and R package 'nmle', version 3.1-115. We report all the measures and variables.

Computational modelling. To investigate whether social presence effects on reaction times are due to the accumulation of information signals or different decision thresholds, we fitted a LATER model to the saccadic reaction time data as seen in Figure 1. LATER is a decision

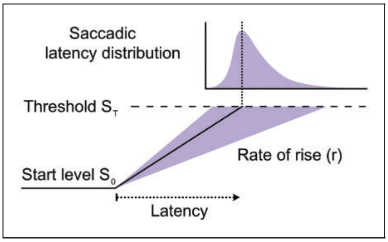

Figure 1. The LATER model. When a stimulus is presented, a decision signal *S* rises linearly from an initial level S_0 at a rate *r*; when *S* reaches the threshold S_T, a saccade is initiated. The rate of rise *r* obeys a Gaussian distribution, which gives a skewed distribution of latencies. Adapted from Gold & Shadlen, 2007.

model based on the concept that responses, such as saccades, follow a decision-making mechanism (Carpenter, 1981; Carpenter & Williams, 1995). When a stimulus is presented, the model predicts that a decision signal (*S*) increases from a baseline S_0 at a certain rate *r* until it reaches a decision threshold S_T that constitutes a criterion level (Carpenter, 2012; Carpenter & Williams, 1995; Gold & Shadlen, 2007; Reddi & Carpenter, 2000) where a decision to take action occurs, for instance, a saccadic movement towards a target. Specifically, the latency t_i of any trial is given by $t_i = (S_T - S_0)/r_i$. As this equation shows, different reaction times can result from varying either the difference between thresholds $S_T - S_0$ or the mean rate of rise μ. Since in the LATER model *r* is assumed to follow a Gaussian distribution, the latency *t* is said to follow a recinormal distribution and the reciprocal of the latency $1/t$ is normally distributed. As a consequence, a straight line is obtained if the cumulative distribution of the reciprocal of the latencies is plotted on a probit axis (a reciprobit plot), with median $(S_T - S_0)/\mu$ and an intercept in the infinite-time axis at $\mu/\sigma\sqrt{2}$, where σ is the standard deviation of *r*.

As plotted in Figure 2, altering S_0 or S_T causes the line of the reciprobit to swivel about a fixed intercept on the infinite-time axis (see Carpenter & Williams, 1995; Reddi & Carpenter, 2000). In contrast, a change in μ causes a parallel shift of the reciprobit line (Reddi et al., 2003). Here we used this model to determine whether any changes in the saccadic latency we observed are due to a shift in the decision thresholds or due to a change in the rate of increase of the decision signal. Specifically, this was assessed by fitting a linear mixed effects model to the saccadic latency data of the two social conditions in probit spaces. For this fit, random intercepts and slopes for each participant were included in the model. The paucity of points in the tails of the distributions can make fit outcomes unstable. For this reason, and consistent with previous research (Harwood, Madelain, Krauzlis, & Wallman, 2008), we limited saccadic latencies included in this analysis to 400 ms. In contrast to Harwood et al. (2008), who used only 68% of the data (one SD surrounding the median), our criterion included 95% of the saccadic latency data in the analysis.

Results

Average pro- and antisaccade latencies are plotted for the group and individual conditions in Figure 3. Correct antisaccades were consistently slower than prosaccades, in both the solitary condition ($b = 1.15$, 95% CI [0.84, 1.47], $t(38) = 7.24$, $p < 0.001$) and the group condition

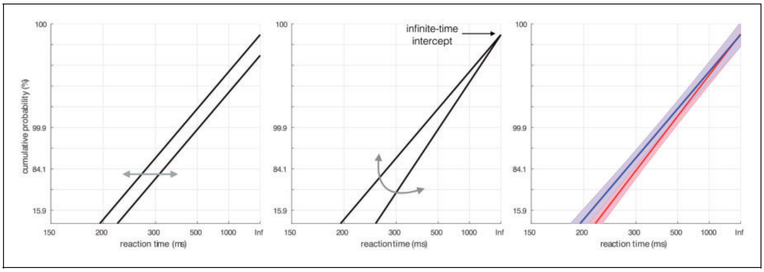

Figure 2. Reciprobit plots. The cumulative distributions of saccadic latencies are plotted on a probit scale with a reciprocal time axis. Left: an increase in the rate of rise of the decision signal would cause a parallel shift. Middle: an increase in S_T will result in a swivelling of the line about the infinite-time axis. Right: the effect of the social conditions on the antisaccadic latency distributions. The group condition had a steeper line (red) than the solitary condition (blue), indicating an increase in the decision threshold. Note that for visualization purposes the *x*-axis is extended beyond the range of saccadic latency data used for this fit to show the intercept with the infinite time axis. The shaded areas represent the 95% confidence intervals.

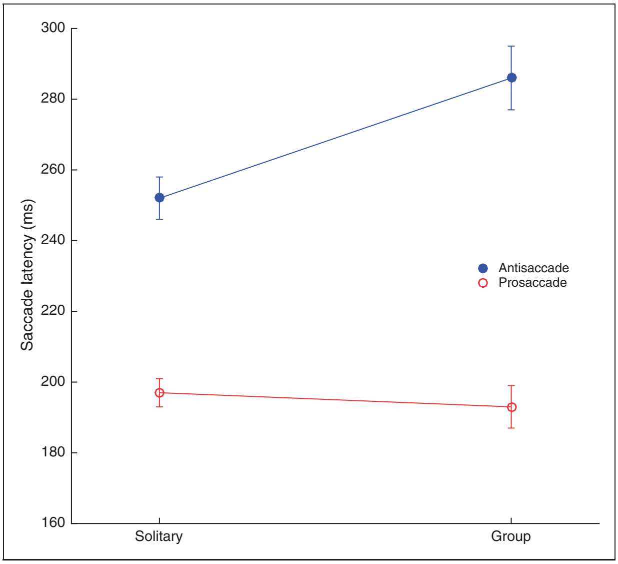

Figure 3. Pro- and antisaccadic latencies for the group and solitary conditions. Error bars indicate standard errors of the mean.

Table 1. Mean ± SE of Corrective Saccadic Latencies for Antisaccades and Saccadic Amplitudes (in Visual Angles) for Pro- and Antisaccades.

	Corrective Saccadic Latency (ms)	Prosaccadic Amplitude (°)	Antisaccadic Amplitude (°)
Solitary	167 ± 13	9.41 ± 0.10	9.52 ± 0.78
Group	184 ± 8	9.59 ± 0.13	9.32 ± 0.52

($b = 1.74$, 95% CI [1.43, 2.01], $t(38) = 16.89$, $p < 0.001$). The antisaccade latency in the group condition (mean ± SEM: 286 ± 9 ms) was higher than in the solitary condition (252 ± 6 ms; $b = 0.45$, 95% CI [0.10, 0.78], $t(38) = 2.73$, $p = 0.008$, $d = 0.92$). In contrast, prosaccade latencies did not differ between the group (193 ± 6 ms) and solitary conditions (197 ± 4 ms; $b = -0.18$, 95% CI [−0.52, 0.16], $t(38) = -1.06$, $p = 0.291$, $d = 0.18$).

The average percentage of correct prosaccades was 99.5% in both social conditions; this low percentage of direction errors is expected as the prosaccade is a simple, automatic response. The average percentage of correct antisaccades was 81.4 ± 2.2% in the solitary condition and 80.3 ± 2.3% in the group condition, which is in line with the error rates usually found for adults in this task (Hutton & Ettinger, 2006). There were no differences in the numbers of incorrect antisaccades between conditions ($t(38) = -0.46$, $p = 0.65$).

Independent-samples t-tests were conducted to compare saccadic gain and the latency of corrective saccades between the group and the solitary conditions (see Table 1). However, the results indicated that there were no significant effects in either analyses ($p > 0.10$ in all cases). The temporal resolution of the eyetrackers used did not allow us to assess differences in dynamic properties like peak saccadic velocities.

Group size effect

To analyse in more detail what effect the presence of others has on antisaccade performance, we investigated how the group size, defined as the number of participants per session, influenced saccade latencies. Pro- and antisaccade latencies as a function of group size are plotted in Figure 4. Consistent with the results presented above, a mixed effects linear regression between the group sizes and the pro- and antisaccade latencies showed that antisaccade latencies increased with group size ($b = -0.11$, 95% CI [−0.20, −0.02], $t(38) = -2.51$, $p = 0.016$). The approximate parameter b indicates that the antisaccade latency should increase 7 ms for every additional participant in the session. Prosaccadic latencies, on the other hand, were not affected by the size of the group ($b = 0.05$, 95% CI [−0.03, 0.14], $t(38) = 1.29$, $p = 0.204$). The data furthermore suggest that the effect of group size on saccadic latency may be better described by a power law function (Figure 4), as proposed by Latane (1981). This issue is further discussed in the general discussion.

Computational modelling

The LATER model allows investigation of the underlying cause of the increase in latencies found in the antisaccade task. Specifically, an increase in latency can have two underlying causes: an alteration in the mean rate of increase of the decision signal μ or a change in the difference between the decision thresholds $S_T - S_0$.

Figure 2 shows example reciprobit plots of saccadic latency data and illustrates how changes of the LATER model's parameters are reflected in the reciprobit plot. A change

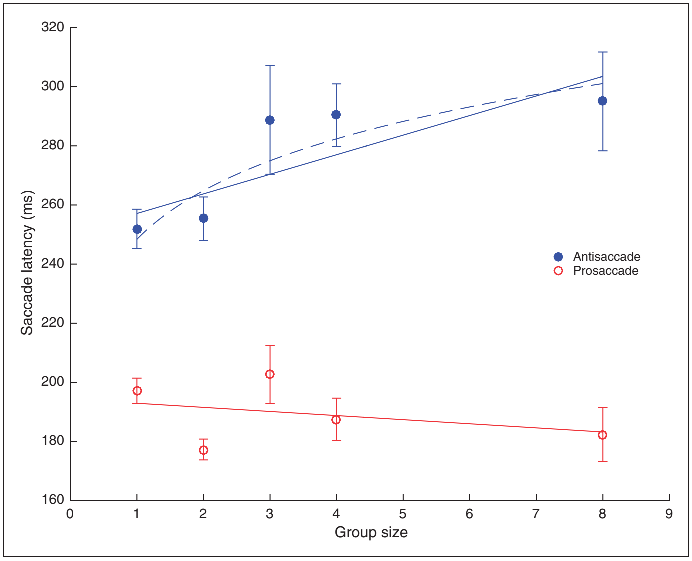

Figure 4. Antisaccade and prosaccade latencies plotted against group size. The dashed line represents a power law fit as predicted by Latane's social impact theory. Error bars indicate standard errors.

in the mean rate of increase of the decision signal μ causes a parallel shift of the reciprobit line, which is reflected in a change of the intercept combined with a slope that does not change. In contrast, a change in the difference between the decision thresholds $S_T - S_0$ leads to a change of the slope but not of the intercept, which appears as a swivel of the reciprobit line about a fixed intercept on the time-infinity axis.

To assess whether the slope or the intercept of the reciprobit line differed between social conditions, we fitted the reciprocal of the saccadic latency data to a mixed effects model. Figure 2 shows the mean fit for each social condition. We found that while the intercept did not differ between the group and solitary conditions ($b = -0.03$, 95% CI [−0.86, 0.81], $t(38) = -0.07$, $p = 0.94$) the slope showed a trend towards being steeper in the group than in the solitary condition ($b = 0.19$, 95% CI [−0.02, 0.41], $t(38) = 1.71$, $p = 0.08$). One participant was a clear outlier in terms of the fit parameters from the model. The exclusion of only this participant makes the difference in the slopes of the reciprobits significant ($b = 0.25$, 95% CI [0.05, 0.45], $t(37) = 2.51$, $p = 0.01$), while the difference in intercepts remained insignificant ($b = -0.19$, 95% CI [−0.98, 0.60], $t(37) = -0.49$, $p = 0.63$). This participant was not an outlier in terms of the number of errors made or antisaccade latency and thus was kept in the analysis. However, the results strongly suggest that the longer latencies in the group condition can be attributed to a shift in the threshold parameter of the LATER model.

Discussion

The results of Experiment 1 indicate that the antisaccade performance was impaired by the presence of others, while prosaccade performance was independent of the social context. The significant increase in the antisaccade latency together with no increase in direction errors of this response indicates that social presence influences the generation of voluntary behaviour rather than the inhibition control of automatic responses. These results are in line with previous studies assessing the influence of attentional load on saccadic control.

The distraction-conflict theory predicts that the attempt to attend to and process multiple inputs (i.e., both the task and the presence of others) increases attentional load (Baron, 1986). If this were the case, social presence ought to affect performance in line with what previous studies report about saccadic control and attentional load. Indeed, Stuyven et al. (2000) showed that increasing participants' attentional load during the antisaccade task with a concurrent tapping task prolonged their antisaccade latency while prosaccades were not affected. A correct antisaccade requires the completion of two steps: an automatic prosaccade should be inhibited and a controlled saccade away from target should be generated (Olk & Kingstone, 2003). The delay in the antisaccade latencies in the group condition could be caused by an effect in one or both of these two antisaccade steps. A careful analysis suggests that an impairment in the capacity to suppress automatic prosaccades would have led to an increase in direction errors in the group condition, which was not observed. Consequently, we propose that social presence mainly influences participants' capacity to generate controlled saccades rather than their ability to inhibit automatic saccades. This hypothesis is reinforced by the fact that Stuyven et al. (2000) showed that increased attentional load also prolonged the latency of controlled saccades even when there was no need to inhibit automatic behaviour as in the antisaccade.

The similarity between Stuyven et al. (2000) and the results of Experiment 1 suggests that the mechanism by which social presence influences performance is by increasing participants' attentional load. The presence of coactors in the environment may lead participants to monitor their environment more than when they are alone. For instance, Muller et al. (2004) argued that individuals in a group are prone to social comparison. Therefore, by concurrently conducting the experimental task and monitoring the environment, participants would engage in a dual-task activity, increasing their attentional control requirements.

On the other hand, activation theory provides an alternative explanation to social influences, stating that social presence increases the likelihood of deploying automatic, dominant behaviour. In the case of the antisaccade task, prosaccades are clearly automatic responses (Roberts et al., 1994) and, therefore, we expected facilitation in the prosaccades, probably reflected by reduced latencies. Since no evidence for such facilitation was found, our data do not support the activation theory. It should be noted that automatic saccades are already rapid responses and it could be physiologically difficult to evidence facilitation by measuring a significant reduction of prosaccade latencies. However, further evidence that prosaccades were not facilitated is provided by the fact that there was no increase in antisaccade direction errors: if the likelihood of a prosaccade as the dominant response increased with social presence, participants should have made more errors trying to suppress prosaccades in favour of antisaccade responses.

Next, we analysed the saccadic latency distributions between social conditions with the LATER model. The results indicated that social presence led to delayed antisaccadic latencies in the group condition due to an increase in the decision thresholds rather than a change in the rate of rise of the decision signal. The decision thresholds relate to the criterion level (e.g., Carpenter & Williams, 1995; Reddi & Carpenter, 2000) at which saccades are executed. The saccadic procrastination, observed in the increased saccadic latency, accounts for the period when sensory information is integrated to decide where to attend and saccade to (Carpenter, 1981). This time window is part of a selection mechanism to control saccades when there are conflicting alternative targets (Schall & Hanes, 1993, 1998; Schall & Thompson, 1999). If participants are in a social environment and attention is allocated to more stimuli, a plausible compensatory mechanism might be to increase the decision threshold to allow more information to be integrated before the saccade away from target is initiated. In that sense, the increased decision threshold may allow for the correct inhibition of reflexive responses, even when the presence of coactors adds extra stimuli to the environment.

In order to investigate whether the same effect of social influence extends to other cognitively mediated responses, we conducted a second experiment that involved both saccades and manual responses.

Experiment 2

Saccade responses are evoked faster than manual responses (Jaśkowski & Sobieralska, 2004) and there seem to be differences in the attentional control required for saccadic and manual responses (Ludwig & Gilchrist, 2002). In Experiment 2, we measured whether saccades are especially sensitive to social context, or whether manual responses are also influenced by the presence of coactors. We used a visual discrimination task that required participants to both make a saccade towards a target (targets were presented at varying distances in the periphery), and a manual response to indicate the orientation of that target. We measured two performance indicators: the saccadic latency of the saccade towards the target and the manual response time in reaction to the visual discrimination.

Methods

Participants and design. As in Experiment 1, this experiment used a 2×2 mixed design (social condition vs response type, i.e. saccadic and manual responses). Experiment 2 was performed after Experiment 1. Therefore, the same participants took part and were assigned to the same conditions as in Experiment 1, and there was no opportunity for them to interact with one another between testing sessions. Two participants were excluded for having a high error rate (nearly chance performance); all other participants had error rates lower than 10%. Ten participants were excluded due to data loss (see 'Data analysis'). The resulting numbers of participants included in the analysis were 21 in the group condition and 19 in the solitary condition.

Stimuli and material. A fixation cross was presented in the centre of the screen for a randomized interval of 60 to 140 screen refresh cycles (1000 ms to 2333 ms). Subsequently, a target was presented in a random position on the screen but at one of 10 possible distances from the centre. The presentation of the target occurred within a minimum radius of 5.4° and a maximum radius of 11.7°. The minimum radius was set in order to avoid recognition of the target through parafoveal vision and with the purpose of inducing a saccadic response. The space between the minimum and maximum radii was divided in eight sub-radii on which the target could be presented. Therefore, each trial required the generation of a saccade to one of 10 possible distances from the centre. There were 15 trials for each of the 10 radii, making a total of 150 trials.

The target consisted of a copyright symbol © displayed at a size of 1.4°. It could be presented as is or flipped horizontally, in which case the opening of the inner 'c' pointed towards the left. One of the two possible orientations was presented for every trial and the task consisted of reporting, as fast and accurately as possible, the orientation of the target, using the left and right arrows on the keyboard and using the dominant hand.

Apparatus. The research settings, hardware and software utilized for Experiment 2 are all the same as in Experiment 1.

Procedure. The procedure was similar to that of Experiment 1. A visual search task was added as a filler at the end, in order to ensure that all participants could finish the experimental task without disturbances.

Data analysis. The saccade onsets were calculated with the event detector and criteria described in Experiment 1. Only participants with more than 70% usable data were included in the analysis. Manual response times above 2.5 SD over the mean were excluded. All participants had error rates lower than 10%. The data were analysed with linear mixed models, allowing random slopes and intercepts for participants. As in Experiment 1, the reciprocal of the saccadic and manual reaction times was used for all analyses.

Results

Figure 5(a) shows the mean saccadic latency as a function of target eccentricity for the group and solitary conditions. Linear mixed effects modelling revealed that while saccadic latencies varied with target eccentricity ($b = -0.06$, 95% CI [−0.09, −0.04], $t(358) = -4.64$, $p < 0.001$), they did not differ between the two social conditions ($b = -0.009$, 95% CI [−0.44, 0.42], $t(38) = -0.04$, $p = 0.96$) and their interaction did not reach significance ($b = 0.02$, 95% CI [−0.01, 0.07], $t(358) = 1.20$, $p = 0.23$).

After making a saccade towards the target, participants had to report the orientation of the target. Manual response times are plotted in Figure 5(b) as a function of target eccentricity for the group and solitary conditions. Linear mixed effects modelling revealed that response latencies increased as a function of target eccentricity ($b = -0.02$, 95% CI [−0.02, −0.01], $t(358) = 7.58$, $p < 0.001$). Manual response latency did not differ between the social conditions ($b = 0.12$, 95% CI [−0.02, 0.27], $t(38) = 1.56$, $p = 0.11$) and the interaction between target eccentricity and social condition did not reach significance ($b = -0.004$, 95% CI [−0.01, 0.003], $t(358) = 1.07$, $p = 0.29$).

Group size effect. Linear mixed effects modelling revealed that while saccadic latencies varied across target eccentricities, they did not differ as a function of group size ($b = 0.02$, 95% CI [−0.09, 0.14], $t(38) = 0.39$, $p = 0.69$). Furthermore, the interaction between target eccentricity and group size did not reach significance ($b = -0.005$, 95% CI [−0.018, 0.002], $t(358) = 1.16$, $p = 0.24$).

In Experiment 1, the average antisaccade latency increased with the number of coactors in the session. In order to see whether the effect on the manual response times could also be moderated by group size, the same analysis as in Experiment 1 was conducted. Linear mixed effects modelling revealed that there was a significant increase in latency as a function of group size ($b = -0.04$, 95% CI [−0.08, −0.02], $t(38) = -2.22$, $p = 0.03$), indicating that participants in bigger groups made slower manual responses. The interaction between

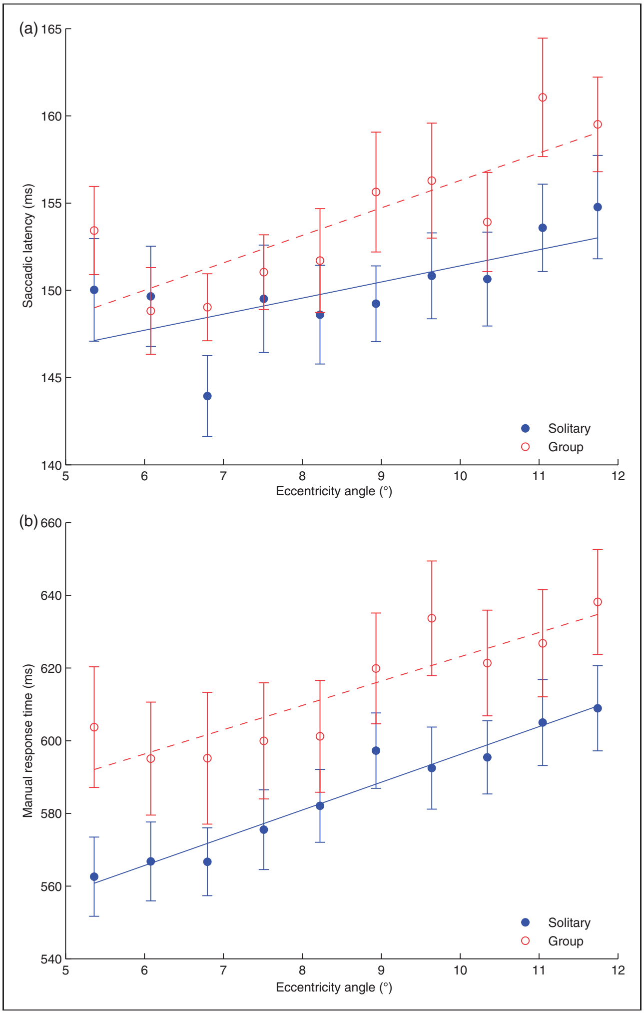

Figure 5. Saccade latencies and manual response times. (a) Saccadic reaction times in the group and solitary conditions were not significantly different. (b) Manual responses in the group condition tended to be slower across the entire range of eccentricities. Trend regression lines are shown for each of the conditions. Error bars indicate standard errors.

target eccentricity and group size did not reach significance ($b = 0.001$, 95% CI [−0.001, 0.003], $t(358) = 1.64$, $p = 0.11$).

In summary, the saccade responses were independent of group size, while the manual response time increased significantly, with slower reaction times for bigger group sizes.

Discussion

The choice reaction time task requires a reflexive response – the saccade towards the target – and a controlled component consisting of the discrimination of the stimulus. We measured saccadic and manual response times to differentiate between these simple and complex components of the task

The first step in the visual discrimination task, the saccade towards the target, is an automatic response analogous to a prosaccade where gaze is directed to an abruptly appearing target. In line with the results of Experiment 1, the saccadic latencies towards the visual target were not affected by the social environment. In contrast to Experiment 1 (antisaccades), the controlled responses in Experiment 2 (manual responses) were not clearly affected by the type of social context. On average, responses were 32 ms slower in the group condition than in the solitary condition, but this difference was only marginally significant. However, the size of the group had a significant effect on the manual reaction times, suggesting that social presence still elicited some influence on cognitively controlled manual responses.

The distraction-conflict theory supposes that the attentional conflict elicited by social presence focuses attention. Baron (1986) also extends this assumption to cues that are most visually central to the task. We assessed spatial narrowing through the saccadic latencies to targets presented at different eccentricities. We expected that a narrowing of the attentional window would prolong saccadic latencies towards targets presented farther away from centre. The results showed that social condition and eccentricity levels had no effect on saccadic latencies, suggesting that there was no such spatial narrowing. However, the eccentricity range analysed was from 5° to 12°; any potential focusing of attention on a more central area (< 5°) should be assessed in the future.

The effect of social influence may not only be restricted to a spatial narrowing of attention but also to other forms of attentional focusing such as the range of cue utilization or use of global and local information (e.g., Navon task). This offers interesting avenues for future research.

General Discussion

We investigated how social presence affects saccadic and manual responses. Our main finding was that social presence had a significant effect on the generation of volitional saccades, but had no effect on automatic saccades. In contrast, a marginally significant effect was reported for controlled manual responses, but increasing group sizes moderated slower reaction times. Altogether, we assume that the group condition affects only controlled responses, presumably due to an increase in attentional load elicited by the presence of others. These results support the view that attentional processes are involved in the mediation of social influences. According to the LATER model analysis, the prolonged latencies can be explained in terms of an increase in the decision threshold, indicating that under social presence, more accumulation of evidence is required before a decision to trigger a controlled response is made.

The distraction-conflict theory states that social presence competes for cognitive and attentional resources with the task at hand. Since attentional capacity is limited, as demands for attention increase less spare capacity remains for other activities. Baron (1986) extended his theory not only to social stimuli but any stimuli that would withdraw attention from the main task. In fact, Stuyven et al. (2000) studied the effect of dual-task interference on the antisaccade task, specifically to assess the effect of attentional and cognitive load on automatic and controlled saccades. In those experiments, participants conducted an antisaccade task concurrently with a tapping task, but participants received different instructions regarding the importance of the secondary task. When the tapping task was less relevant to the overall performance, no effect on the antisaccades was observed. However, by instructing participants to keep a good tapping performance, the authors reported an increase in antisaccadic latency but not prosaccade latency. In other words, the amount of monitoring that participants allocated to the secondary task influenced the generation of only controlled saccades.

If there is an urge in individuals to monitor the social context when others are present, a similar analysis to that above can be performed when studying social influences. According to our results, this increased demand affected the generation of volitional responses, but did not impair the ability to suppress automatic behaviour when required, as evidenced by unchanged error rates. A relevant question now is *why* participants allocate attention to the environment when others are present. Previous studies suggest that the possibility for social comparison and adequacy to a social standard contributes to participants' desire to monitor the social environment. Zajonc (1980) proposed that social presence increases individuals' alertness because social presence adds uncertainty to the environment. The hypothesis was further developed by Guerin and Innes (1982), who suggested that task performance is affected when others cannot be visually monitored, or when others are unpredictable. Cottrell, Wack, Sekerak, and Rittle (1968) proposed that performance will change only when participants assume that they can be evaluated by others; however, this was later found not to be necessary for social facilitation–inhibition (Bond & Titus, 1983). Alternatively, Sanders et al. (1978) suggested that others provide social comparison information that can moderate social presence effects (Huguet et al., 1999; Muller et al., 2004). However, an implicit presence can also affect the deployment of social attention (Risko & Kingstone, 2009). Besides this, it was also proposed that certain personality traits moderate the general orientation of individuals towards the social environment (see Aiello & Douthitt, 2001, Strauss, 2002, and Uziel, 2007, for reviews). Carver and Scheier (1981) proposed in their feedback-loop model that social presence leads individuals to direct attention to the self in order to assess their own behaviour. This feedback-loop process may help participants to correct their behaviour and improve performance. However, self-attention can also interfere with the behavioural task and impair performance. This hypothesis also proposes an attentional mediation of social effects, but differs from the distraction-conflict theory in that attention is directed inwardly to the self rather than outwardly to the social environment. See Guerin (2010) for a review of social facilitation theories and findings.

As described, there are several potential reasons for why participants would engage in monitoring of the environment when others are present. An emerging question is *how* this attention to the environment is regulated. Attention to the environment could be driven by a volitional, controlled process or by a bottom-up, reflexive response. In this regard, the distraction-conflict theory refers to social presence as a distraction that competes for attention. The idea of distraction resembles a bottom-up type of influence. However, it could also be the case that individuals engage in an active monitoring of the social environment. Our view is that this process could be mediated by an interplay between volitional monitoring and bottom-up processes. Social presence might elicit a reflexive response that leads to the active monitoring of the environment. For instance, it could be that the urge for social comparison is a bottom-up process, but that the means by which individuals monitor the environment is achieved by top-down mechanisms. Further research should assess whether the potential causes mentioned above should be considered as bottom-up or top-down processes.

Dual-task experiments also showed that if the secondary task is excessively demanding, it can also impair the suppression of automatic saccades and increase direction errors. Roberts et al. (1994) studied the effect of dual tasks on the antisaccade with a concurrent task in a similar way to Stuyven et al. (2000), but with a more demanding interference task. Roberts et al. (1994) had participants listen to numbers, then perform an arithmetic calculation and verbalize the result. In contrast to Stuyven et al. (2000), Roberts et al. (1994) reported a significant increase in direction errors in the antisaccade task. Indeed, studies have shown that attentional depletion, caused by taxing the working memory capacity, affects individuals' ability to suppress automatic saccades (Mitchell, Macrae, & Gilchrist, 2002). If interference disrupts the active maintenance of the task goals, diverted attention will lead to the deployment of automatic behaviour.

In a similar vein, cognitive distraction has also been found to interfere with the active maintenance of the task goals. For instance, Halliday and Carpenter (2010) explored the effects of cognitive distraction with a go/no-go saccadic task compared to a control group without distraction. This task again requires the inhibition of a saccade in the no-go trials. When participants were presented with bursts of pink noise concurrently with the task, neither the saccadic latency nor the direction error rates were affected. However, when participants performed a concurrent antonym verbal task, this led to higher direction error rates compared to the control group. Such results differ from the ones presented here in that inhibitory capacity was unaffected by our manipulation; rather, participants had prolonged response preparations. More examples where there is a deficit in response inhibition are provided by patients with attention-deficit hyperactivity disorder (ADHD). In a review, Munoz and Everling (2004) describe that what characterizes ADHD patients in the antisaccade task is increased direction errors, while correct antisaccades display normal reaction times, implying that they have no deficit in the capacity to initiate voluntary responses.

Thus, a reasonable interpretation would be that if you have a mild secondary task that you can handle, latencies but not direction errors are affected, but if the secondary task is very demanding, it can also affect direction errors. In our study, the effect of social presence specifically affected the generation of controlled saccades, suggesting that the coactors' influence might be attributed to the engagement of participants in a mild dual-task activity by concurrently monitoring the environment.

The analysis conducted with the LATER model suggested that the response to social presence led to an increase in the decision thresholds. The functional significance of a change in the threshold parameters of the model has been assessed by Reddi et al. (2003) and Reddi and Carpenter (2000) in studies that investigated the effects of urgency and accuracy on saccadic responses. By asking participants to saccade either as fast or as accurately as possible towards a target, the authors showed that the decision threshold moved depending on the instructions. Faster response times were achieved by lowering the decision threshold, in which case the decision signal reached the criterion level to initiate a saccade in a shorter amount of time. In contrast, higher accuracy was achieved by increasing the decision threshold, so that more accumulation of the decision signal was required in order to initiate a saccade. If the environment becomes more uncertain with social presence, the selection mechanisms that decide where to allocate attention should also respond to such additional stimuli. In response, a plausible adaptation might be achieved by increasing the decision threshold that we found, allowing for more sensory integration before making the decision on where to saccade.

The other parameter of the model, the decision signal, characterizes the speed of acquisition of information about the stimulus (see Nouraei, de Pennington, Jones, & Carpenter, 2003; Reddi et al., 2003). We expected that this parameter could change if there were differences in the speed of processing elicited by the influence of the social environment (e.g., cognitive distraction that would slow down processing). However, no such result was found.

The comparison between solitary and group conditions showed that manual responses were only marginally affected by social presence. Such results contrast with the significant effect found for controlled saccades. Some differences between these responses might account for why social presence affected them differently. For instance, manual responses have significantly larger latencies than saccadic eye movements (Jaśkowski & Sobieralska, 2004; Ludwig & Gilchrist, 2002) and saccades have been shown to be more affected by attentional overload than manual responses are (Ludwig & Gilchrist, 2002). Therefore, saccadic responses should better reflect early processes of attention selection, while the longer latencies of the manual responses might allow for more sensory integration before an action is taken. Saccades occur at a rate of two to three times per second in humans (Holmqvist et al., 2011), while manual responses in reaction to visual stimuli are scarce in comparison. Additionally, in the antisaccade task, the correct volitional response is in competition with a more reflexive – but erroneous – prosaccade. In contrast, no inhibitory control is required in the manual responses of Experiment 2. These additional attentional demands in the antisaccade task may account for why such responses are more sensitive to, for example, attentional load, than manual responses when others are present.

In both of our experiments, the number of people present in the recording session had a significant effect on performance change. A larger number of coactors may reinforce individuals' awareness of the social presence and, hence, moderate the extent to which attention is allocated to the environment at the expense of attention used for the experimental task. Latane (1981) proposed that a crowd (or an audience) of a determined size (N) will have an *impact* (I) on an individual's behaviour that can be described as a power law function of the form $I = sN^t$, with s being a constant and the exponent t being lower than one. The function describes an increase in social impact with group size that eventually flattens out with bigger crowds. Although the theory prediction does not always hold (Argo, Dahl, & Manchanda, 2005), our results seem to be consistent with Latane's social impact theory. The relationship between group size and the increase in the antisaccade latencies seems to flatten out (Figure 4). The best-fitting power function calculated accounts for 59% of the variance in means (better than the 43% best linear fit). It is worth noting that Latane's theory relates to crowd or audience conditions, whereas we used a coaction manipulation. Therefore, it is advisable to further study the role of group size in more dedicated experiments.

The present study focused on how the presence of coactors influenced saccadic and manual responses. Participants in our experiments were not required to compete and did not receive explicit interaction instructions. In this sense, our results constitute a baseline measure of how attentional control is affected by conditions of coaction. For this purpose, eye movements proved to be a successful novel strategy for the study of the attentional effects of social influences. This should open up the door to future studies investigating participants' attentional control under different manipulations (e.g., competition, evaluation, cooperation) that may lead to novel findings.

Conclusions

In conclusion, the present study provides evidence for an attentional view of coaction effects. Even when participants are not directly interacting with each other, the presence of coactors seems to consume attentional resources that affect controlled saccadic responses but not automatic saccades. Manual responses were not affected by the social context, probably due to the fact that saccades can be evoked more rapidly than manual responses. However, the number of coactors in the group moderated the change in performance for both controlled saccadic and manual responses. The analysis of latency distributions with the LATER model indicates that the delayed saccadic latencies in the group condition are due to an increase in the decision threshold of when to initiate a response.

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Paper II

Groups do it better? Social influences on computer-based learning

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Abstract

This study investigated whether the presence of other students influences learning outcomes compared to when students perform in solitary. The influence of the social context was assessed within two computer-based multimedia learning tasks, where participants had to learn from texts and illustrations. Participants completed the experiment either in solitary or under the presence of other students who each conducted the same experiment individually. Previous studies show that social presence can either enhance or impair cognitive performance depending on the attentional demands of the task at hand. Therefore, here we studied whether the difficulty level and the instructional design of a learning task can interact with the type of social environment to moderate learning performances. Multivariate analyses indicated that the presence of other students led to higher learning performances across post tests. Participants in the group condition obtained higher transfer scores in both learning tasks, whereas retention performance improved only in one task. Furthermore, the analysis showed that the number of learners in the group (the group size) may moderate the effect of social presence. The study shows that social presence can significantly impact learning performances, even when working individually on computer-based tasks.

Keywords

Social Presence; Social Facilitation; Multimedia Learning; Learning Environment; Computer-based Learning.

1. Introduction

Educational research is either conducted within educational practice (highly ecologically valid but with little control) or under strict laboratory conditions, where participants complete learning tasks and evaluations in solitary, isolated conditions (highly controlled but little ecologically valid). This constitutes a sensible methodological strategy in order to constrain the factors that are specific to the respective research questions. However, a vast percentage of the learning processes take place in social environments such as classrooms, libraries or study groups where students are immersed in social environments. Previous research in education has studied social interaction effects where students had to cooperate or compete between each other (e.g., Herrmann, 2013; Johnson & Johnson, 2009). However, social experiments have shown that even the mere presence of others can sometimes enhance and sometimes impair performance in different cognitive tasks (Guerin, 2010). Whether social presence will have a positive or negative effect on performance is highly dependent on the attentional demands that the task imposes to the participant. Since it is well known in education that attentional resources are key for understanding and meaningful learning (Mayer, 2002; Paas, Tuovinen, Tabbers, & Van Gerven, 2010; Sweller & Sweller, 1994), the aim of the present study is to investigate whether the presence of other learners, even when they are not directly interacting with each other, can also influence learning performances compared to when participants perform alone.

It has been previously reported that the sheer presence of other people influences the individual's attention and actions (Zajonc, 1965). In particular, performing the same task at the same time with other coactors has been shown to sometimes facilitate and sometimes inhibit performance compared to when individuals perform alone, and this dynamic is known as *social facilitation-inhibition* (Bond & Titus, 1983; Zajonc, 1965). Recent studies showed that social presence effects are mediated by attentional processes (Chajut & Algom, 2003; Huguet, Galvaing, Monteil, & Dumas, 1999; Muller, Atzeni, & Butera, 2004; Oliva, Niehorster, Jarodzka, & Holmqvist, 2017). The distraction-conflict theory (Baron, 1986; Sanders, Baron, & Moore, 1978) of social influence postulates that the presence of other people competes for attentional resources, causing that less capacity remains available for the task at hand. As a consequence attention becomes restricted to a smaller set of elements (Cohen & Spacapan, 1978). Interestingly, by preventing the use of irrelevant cues, this focusing of attention can facilitate performance on simple tasks that require the use of a small set of elements (Huguet et al., 1999; Muller et al., 2004). On the contrary, complex tasks usually require the use of a larger range of elements. In this latter example, attentional focusing would impair performance if relevant information results neglected. Therefore, according to the distraction-conflict theory, social presence can have divergent effects on performance depending on the nature of the task and the attentional requirements involved.

Since attentional resources (and how they are used) are key to successful learning, it is important to understand whether the type of social context can also influence learning performances. In order for a material to be understood, learners must integrate the relevant information into a mental model (Mayer, 2001; Sweller & Sweller, 1994). The cognitive theory of multimedia learning (Mayer, 2014) hypothesizes that the construction of mental models can be fostered when the information is presented in different modalities (e.g., text and illustration). In this regard, *multimedia learning* occurs when a learner is able to build mental representations from texts and illustrations. This process requires to establish integrative connections between the verbal information from the text and the relevant graphical features from the visual information (Mayer & Moreno, 2003; Paivio, 1990). Eye tracking research, for instance, showed that high ability students not only spend more visual attention to relevant parts of the learning material but also make more integrative saccades between these relevant parts (Hannus & Hyönä, 1999; Holsanova, Holmberg, & Holmqvist, 2009).

The integration of information utilizes attentional and cognitive resources, but only a limited amount of cognitive processing can take place at any one time (Chandler & Sweller, 1991; Paas, Fred; Renkl, Alexander; Sweller, 2004; Sweller & Sweller, 1994). If the cognitive demands of the task at hand exceed the cognitive capacity of the learner, this leads to cognitive overload and impairs learning. For instance, multimedia material can be presented in *integrated* or *split* layouts. In the split format the text and the illustrations are presented separately and the learner has to engage in a search for referents that imposes extraneous, incidental processing. On the other hand integrated designs already present text and images in layout that reduces activities that are irrelevant for learning. It has been shown that, usually, materials are assimilated more rapidly when presented in integrated rather than split formats, with higher subsequent test performance levels (Chandler & Sweller, 1991 Chandler & Sweller, 1992; Purnell, Solman, & Sweller, 1991).

Although the interplay between cognitive functions and learning is largely researched (e.g., Paas, Renkl, & Sweller, 2003; Sigman, Peña, Goldin, & Ribeiro, 2014), little is known whether these cognitive processes can be affected by the type of social context learners are in. Educational studies focusing on social cognition primarily studied conditions of cooperation and competition between students (Johnson & Johnson, 2009; Salomon & Perkins, 1998). These studies showed that cooperating with one or more individuals can lead to better learning performances. However, cooperation in a group can also lead to social loafing (Johnson, Johnson, & Smith, 1998; Salomon & Perkins, 1998) where participants perform below their individual standards. In contrast, the present study focuses on the influence of the social presence when participants complete a learning task together with other students, but working individually and independently from each other, where no cooperation nor competition instructions are given to the students.

1.1 The Present Study

In this study, we test the effect of the presence other students on individual learning performances and discuss our findings in the light of social effects theories. We compare the performance of participants in two social conditions, one in which the participants conducted the experiment in the presence of other co-learners who did the same tasks at the same time (group condition), and another condition in which participants conducted the task in solitary (single condition).

In line with previous social research conducted with different cognitive tasks, we expect the social context to have divergent effects on learning performances depending on the attentional demands imposed by the learning tasks. In particular we set out to test whether manipulating the task difficulty and the instructional design can foster or impair learning compared to when students complete the same tasks but in a single condition. The task difficulty was manipulated by changing the number of element that composed the task. We also manipulated the way this information was presented to the students, which could be either in split or integrated layouts.

When the learning task is simple and requires relatively low attentional demands, we expect that social presence should lead to an enhancement in learning performance. Our first hypothesis is that social presence should have a facilitatory effect on learning performances on simple tasks that involve a small range of elements: A focusing of attention may for instance help to reduce extrinsic cognitive load and potential interference with non-relevant elements of the task. In other words, focusing attention to the main elements of the task should lead to better understanding of the material. From a cognitive load perspective, if the student is using a given level of mental effort, and such resources are focused over relevant elements of a task, this should have a beneficial effect on learning.

In the same way, an increase in task complexity should lead to performance inhibition under social presence. If the task involves a large number of elements or if the interactivity between them is high, attentional focusing can lead learners not to pay adequate levels of attention to all the elements required for schema acquisition. To assess this hypothesis we varied the complexity of the task by manipulating the number of elements required for building the mental model.

The instructional design has also been shown to moderate the cognitive resources required for learning the respective material. Bad material designs that causes a split-attention effect, imposes higher attentional demands and extraneous cognitive load. We investigate whether participants who receive integrated learning materials will get better learning performances than those that receive materials with split layouts.

Lastly, we expect that the difficulty and instructional design should lead to positive and negative interactions. If the type of social context and the instructional design are both beneficial for learning, then a positive interaction between these factors can be expected. In particular, we expect that students in the group condition that receive a simple tasks (social facilitation) in an integrated layout (less incidental processing) will have the best learning performance, since both the material and the group context are said to enhance performance. On the contrary, social presence is said impair performance when tasks are complex (social inhibition). If also the instructional designs imposes higher cognitive demands on learners (e.g., a split design), a negative interaction effect between these factors should be expected.

The results of the study are discussed in the light of different social and learning theories to provide possible explanations why the mere presence of other students can influence individual learning performances.

2. Methods

2.1. Participants and design

Two hundred and nine university students were recruited for this study. Form those, one hundred students participated in the solitary condition ($M_{\text{age}} = 24.4 \pm 3.6$; 36 men) whereas one hundred and nine participated in the group condition ($M_{\text{age}} = 24.1 \pm 3.9$; 55 men). Participants received a movie ticket in return for participation. The experiment used a 2 x 2 x 2 design, with factors and levels being social context (single - group), difficulty (simple - complex) and instructional design (split - integrated).

2.1. Material

Two *multimedia learning tasks* were used. One was about the flow of blood through the human heart, the other one about the working mechanism of a toilet flush system. The material consisted of a text and a picture and it was presented either on an integrated or a split layout, depending the experimental condition (Fig. 1). The complex heart task consisted of 12 anatomical components and the simple condition consisted of a subset of 6 of those 12 components from the complex version. The complex toilet task had two more mechanical components than the simple, and four mechanical components received longer names than in the simple condition.

In the *prior knowledge* tests participants were asked to explain the anatomy and function of the heart. For the toilet task, they had to describe the function of a toilet flush system. Participants wrote their answers in the computers and they were asked to respond as detailed as possible.

In order to assess *retention* after the heart and toilet tasks, participants completed a free recall test where they had to write all what they had learned during the learning phases. The retention question for the heart task was the following: “Please write everything you know about the blood flow through the human heart, detailing the anatomical parts involved”. The retention question for the toilet task was: “Please write everything you know about the working mechanism of a toilet flush, detailing the mechanical components involved”

The *transfer* tests consisted of questions where students had to apply what they had learned in a novel situation or context, and use information that was not explicitly represented in the learning materials. Therefor, transfer tests assess a deeper level of understanding than retention assessment. The transfer questions were: “Decide if the following statement is true or false and explain your reasoning: All arteries in the body transport oxygenated blood” and “Decide if the following statements is true or false and explain your reasoning: The right side of the heart only contains de-oxygenated blood”. The transfer question for the toilet task was: “Describe what would happen with the system and its mechanical components if the flapper would fail to descend back.” In the *labeling* test, participants had to label the same figure they received during the respective learning phase.

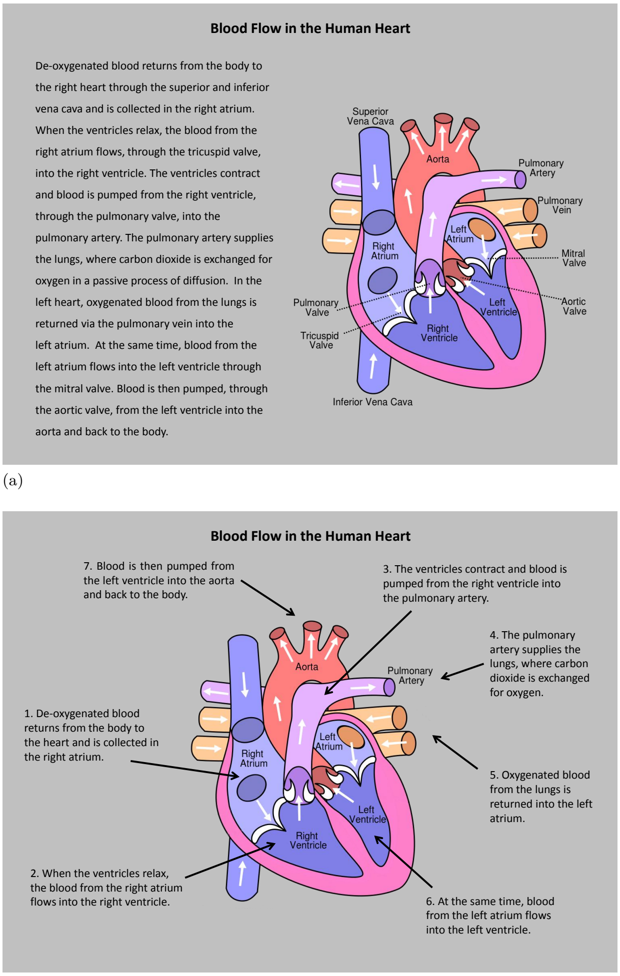
Participants performed an English test (*C-test*; see Raatz & Klein-Braley, 1981) and a memory test (*letter-number sequencing task*; see Crowe, 2000).

2.1.1. Scoring

In the retention test, participants received one point for each anatomical element included in their answer (regardless of wording) and an additional point when the function of such anatomical component was correctly assigned within the system they had to learn. In the transfer questions, participants received two points for a correct true/false answer and up to six additional points for a correct explanation of their response; their transfer scores were then totaled by adding together their scores on each transfer question. Interrater agreement for the transfer tests of 30 participants was sufficiently high for both the heart ($r = .96, p < 0.001$) and the toilet task ($r = .87, p < 0.001$). For the labeling test, participants received one point for each item correctly recalled, regardless of wording. The prior knowledge was scored with the same criteria than used for the retention test.

2.2. Apparatus

The study was performed in a digital classroom (2) equipped with 25 computers (DELL P2210, 1680x1050, 60Hz) where the tables were arranged in a u-shape. The distance between computers was approximately 100 cm and all participants completed the experiment working individually in one computer. The single condition was conducted in the same setting.



Blood Flow in the Human Heart

De-oxygenated blood returns from the body to the right heart through the superior and inferior vena cava and is collected in the right atrium. When the ventricles relax, the blood from the right atrium flows, through the tricuspid valve, into the right ventricle. The ventricles contract and blood is pumped from the right ventricle, through the pulmonary valve, into the pulmonary artery. The pulmonary artery supplies the lungs, where carbon dioxide is exchanged for oxygen in a passive process of diffusion. In the left heart, oxygenated blood from the lungs is returned via the pulmonary vein into the left atrium. At the same time, blood from the left atrium flows into the left ventricle through the mitral valve. Blood is then pumped, through the aortic valve, from the left ventricle into the aorta and back to the body.

(a)

Blood Flow in the Human Heart

7. Blood is then pumped from the left ventricle into the aorta and back to the body.

3. The ventricles contract and blood is pumped from the right ventricle into the pulmonary artery.

4. The pulmonary artery supplies the lungs, where carbon dioxide is exchanged for oxygen.

1. De-oxygenated blood returns from the body to the heart and is collected in the right atrium.

5. Oxygenated blood from the lungs is returned into the left atrium.

2. When the ventricles relax, the blood from the right atrium flows into the right ventricle.

6. At the same time, blood from the left atrium flows into the left ventricle.

(b)

Figure 1. Learning Material Examples. The figures illustrate (a) the learning material for the heart task in the split layout of the complex condition and (b) the integrated-simple version for the same task.

Figure 2. The study was conducted in a digital classroom equipped with 25 computers. Each participant worked individually in one computer in both the single and group conditions. This research setting is also intended for eyetracking research applied to educational sciences.

2.3. Procedure

Participants in the single condition completed the experiment in solitary, without other students present in the room. In the group condition, groups of 2-13 students completed the experiment under the presence of other students. Participants in the group condition were instructed to work individually. All participants took the experiment in the same research facility (a digital classroom) regardless of social condition (group and single). The whole experiment was performed on computers. The experimenter gave a brief oral description of the experiment and subsequent instructions were presented on the computer screens. First, participants performed an English test (*C-test*; see Raatz & Klein-Braley, 1981), a memory test (*letter-number sequencing task*; see Crowe, 2000) and a prior knowledge test. Then, participants proceeded with the learning sessions. During the learning phases, the material was presented on the computer screens for four minutes. The learning tasks (heart and toilet) were presented in counterbalanced order. After each learning phase, participants completed a retention, transfer and labeling tests, with no time limitations. Finally, participants answered questionnaires about mental effort, perceived task difficulty, and those in the group condition were also asked whether social presence affected or influence their performance.

2.4. English Test

There were no differences in English level between the two social conditions ($F(1, 204) = 0.013$, $p = 0.910$).

2.5. Working Memory

There were no differences in working memory capacity between the two social conditions ($F(1, 204) = 0.911$, $p = 0.341$).

2.6. Data Analysis

Data was analyzed with multivariate analyses of variance (MANCOVA) in IBM SPSS (v.22). The linear regressions were conducted using Statsmodels (v.0.6.1) module for python. Following recent recommendations (Norman, 2010), the questionnaire data was analyzed with parametric tests (ANOVA).

3. Results

3.1. Blood Flow Through The Human Heart Task

We conducted a multivariate analysis of variance (MANCOVA) with social context, difficulty, instructional material as factors and the test scores for the recall, transfer and labeling post tests as dependent variables. In the model we controlled for prior knowledge, English knowledge and working memory capacity, which therefore were included as covariates. The analysis revealed no multivariate effect of working memory capacity ($\Lambda_{Pillai} = .002$, $F(3, 194) = .151$, $p = .929$) and, consequently, working memory capacity was excluded from the final MANCOVA model.

The resulting MANCOVA results revealed a significant multivariate effect for social context ($\Lambda_{Pillai} = .036$, $F(3, 197) = 3.736$, $p = .026$), indicating that students in the group condition obtained significantly higher overall learning scores across post-tests. As expected the multivariate effect for task difficulty was also significant ($\Lambda_{Pillai} = .262$, $F(3, 197) = 35.546$, $p < .001$). In contrast, there was no multivariate effect for instructional design ($\Lambda_{Pillai} = .012$, $F(3, 197) = .821$, $p < .484$). No interaction effects were found for social context and task difficulty ($\Lambda_{Pillai} = .005$, $F(3, 197) = .340$, $p = .796$), context and material ($\Lambda_{Pillai} = .016$, $F(3, 197) = 1.062$, $p = .366$), nor triple interaction between difficulty, instructional design and social context ($\Lambda_{Pillai} = .004$, $F(3, 197) = .291$, $p = .832$).

The univariate tests (summarized in Table 1) showed that the social context had a significant facilitation effect on learning outcomes for both the transfer and the recall post-tests: in the transfer test, participants from the group condition averaged $50.86 \pm 2.47\%$ while those in the single condition scored $41.62 \pm 2.77\%$ (see Fig. 3), which resulted in significant differences (Table 1). For the recall test, participants in the group condition scored $60.44 \pm 2.40\%$ whereas those in the single condition averaged $52.79 \pm 2.69\%$, resulting in significant differences between them. For the labeling test, participants in the group condition ($64.37 \pm 3.56\%$) scored higher than those in the single condition ($57.46 \pm 3.99\%$), however this difference did not reach significance levels (Table 1). The effect of social context on all eight conditions is shown in the Figures 4, 5 and 6.

As expected, task difficulty had a significant effect on learning outcomes, where learners in the complex condition obtained significantly lower learning performances than those in the simple condition in all three post-tests (Table 1).

Lastly, the instructional design (split or integrated material) did not have an effect on learning performances for this task (Table 1).

The univariate tests showed that prior knowledge as covariate was a significant predictor of learning outcomes on the three post tests (transfer, recall and labeling; all $ps < .001$). On the other hand, the English score was a significant predictor of performance on the transfer and recall tests ($ps < .001$), but did not predict the label score ($p = .273$).

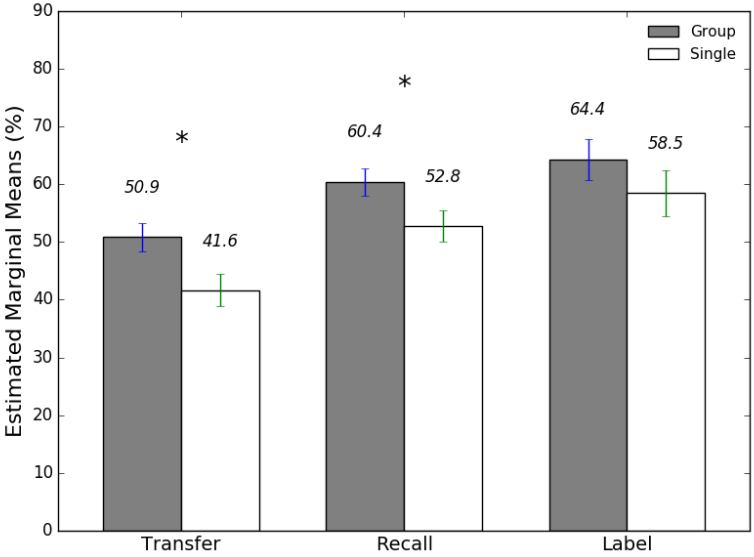


Figure 3. Effect of social context on transfer, recall and labeling scores for the heart task. The numbers indicate means for each task and social condition. Error bars represent standard errors. (*) denotes $p < 0.05$.

3.1.2. Questionnaires

Participants completed a survey where they were asked about the mental effort required for the learning task. The social context ($F(1, 197) = .981$, $p = .323$) and material ($F(1, 197) = 1.037$, $p = .309$) had no significant effect on the perceived mental effort required for the task. The difficulty of the task had a significant effect on mental effort ($F(1, 197) = 7.365$, $p = .007$).

3.2. Working Mechanism of a Gravity Toilet Task

Multivariate analysis of variance (MANCOVA) revealed a multivariate effect for social context ($\Lambda_{Pillai} = 0.048$, $F(3, 197) = 3.283$, $p = 0.022$, $\eta_p^2 = 0.048$), revealing that–consistently with the heart task–students in the group condition obtained significantly higher overall learning scores across post-tests. On the other hand, there were no multivariate effects for difficulty ($\Lambda_{Pillai} = 0.024$, $F(3, 197) = 1.633$, $p = .183$, $\eta_p^2 = 0.024$) and instructional design ($\Lambda_{Pillai} = 0.010$, $F(3, 197) = 0.670$, $p = 0.572$, $\eta_p^2 = 0.010$). No interaction effects were found between social context and task difficulty ($\mathit{\Lambda}_{Pillai} = .003$, $F(3, 197) = .207$, $p = .892$), context and material ($\mathit{\Lambda}_{Pillai} = 004$, $F(3, 197) = .264$,

Source	Variable	$\bar{\Delta}$	$F(1, 199)$	p-value	η_p^2
Social Context	Transfer	9.24 ± 3.77	5.985	**.015**	.029
	Recall	7.65 ± 3.67	4.353	**.038**	.022
	Label	6.91 ± 5.44	1.614	.205	.008
Difficulty	Transfer	-7.43 ± 3.69	4.046	**.046**	.020
	Recall	-29.59 ± 3.58	68.139	$<$ **.001**	.257
	Label	-13.28 ± 5.31	6.110	**.014**	.030
Material Design	Transfer	-5.40 ± 3.68	2.124	.147	.011
	Recall	-2.50 ± 3.58	.417	.519	.002
	Label	0.29 ± 5.31	.010	.922	$<$ .001

Table 1

Univariate statistical results for the heart task. $(\bar{\Delta})$ *denotes the mean score difference between levels (group − single, complex − simple, integrated − split) and the respective standard error.*

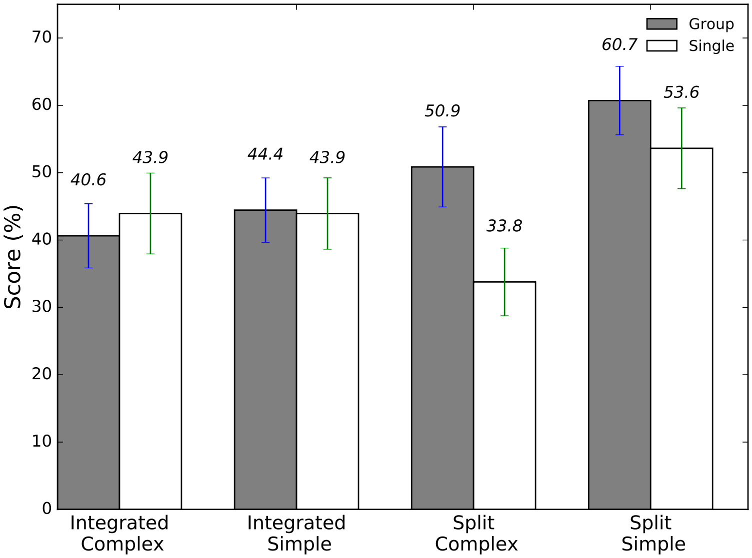


Figure 4. Transfer performances for the heart task. All experimental conditions are grouped by social condition. Error bars indicate standard errors.

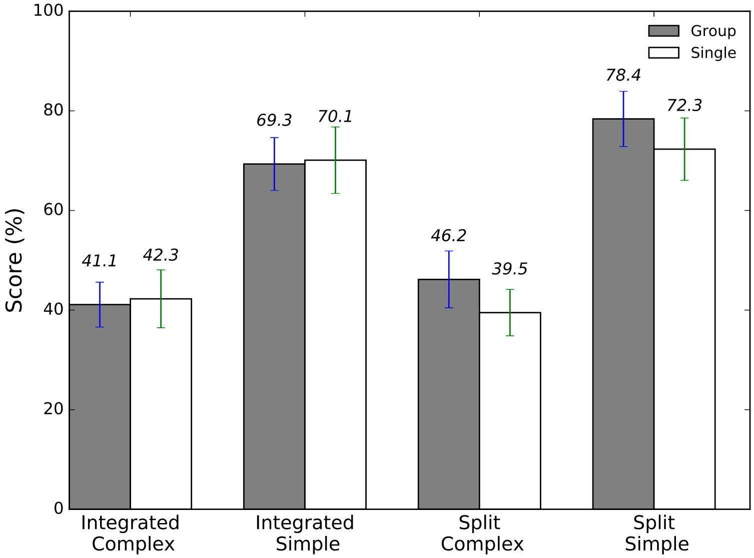


Figure 5. Recall performances for the heart task. Mean recall scores for all conditions. Error bars represent standard errors.

$p = .851$), nor triple interaction between difficulty, instructional design and social context ($\Lambda_{Pillai} = .005$, $F(3, 197) = .827$, $p = .832$).

Table 2 presents the results of univariate analysis of variance (MANCOVA). The univariate tests showed that the social context had a significant facilitation effect on learning outcomes for the transfer post-test. In the transfer test, participants from the group condition averaged $36.22 \pm 1.69\%$ while those in the single condition scored $28.39 \pm 1.97\%$ (see Fig. 10) which resulted on a significant difference (Table 2). For the recall test, participants in the group condition scored $51.24 \pm 1.49\%$ whereas those in the single condition averaged $47.15 \pm 1.74\%$, resulting on marginally significant differences between them. For the labeling test, participants scored $56.69 \pm 1.81\%$ and $55.05 \pm 2.11\%$ in the group and single conditions respectively, however this difference did not reach significance levels (Table 2). Figures 7 and 8 detail the effect of social context for the transfer and recall test for all experimental conditions.

Task difficulty had a significant effect on transfer outcomes, where learners on the complex condition obtained lower performances than those in the simple condition (Table 2). However, there was no effect of difficulty on recall and labeling performances (Table 2).

Finally, the instructional design (split or integrated material) did not have an effect

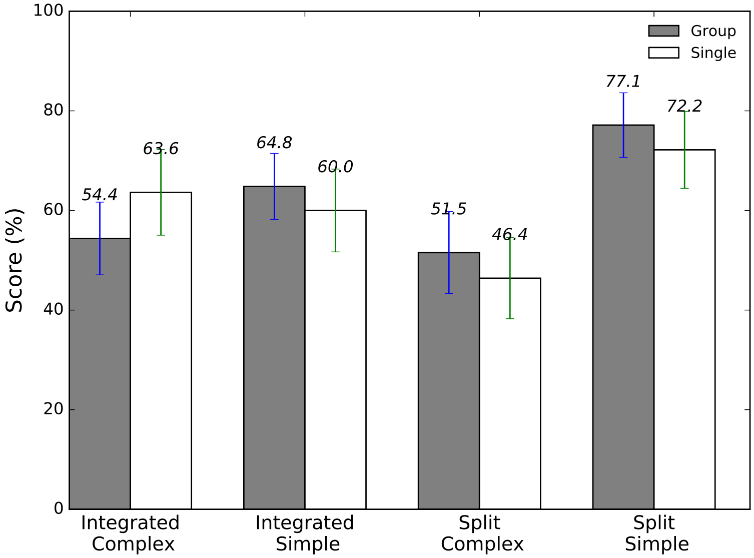


Figure 6. Labeling performances for the heart task. Error bars represent standard errors.

on learning performances for this task (Table 1).

As for the heart task results, univariate tests showed that prior knowledge as covariate was a significant predictor of learning outcomes on the three post tests (transfer, recall and labeling; all $ps < .001$). English knowledge was a significant predictor of performance on the transfer and recall tests, but in contrast to task 1, it was also a significant predictor of the label score (all $ps < .001$).

3.2.1. Questionnaires

There were no differences for the reported mental effort for context ($F(1,199) = .015$, $p = .910$), instructional design ($F(1,199) = .646$, $p = .423$) and difficulty ($F(1,199) = .114$, $p = .736$).

3.3. The Size of the Group

Participants assigned to the group condition completed the experiment in sessions that differed in the number of participants present. It could well be the case that the influence of the social environment is related to the size of the group. Therefore, we assessed whether the number of individuals in the group would moderate the effect of the social context. In order to do this, we performed linear regressions between the total scores obtained by the

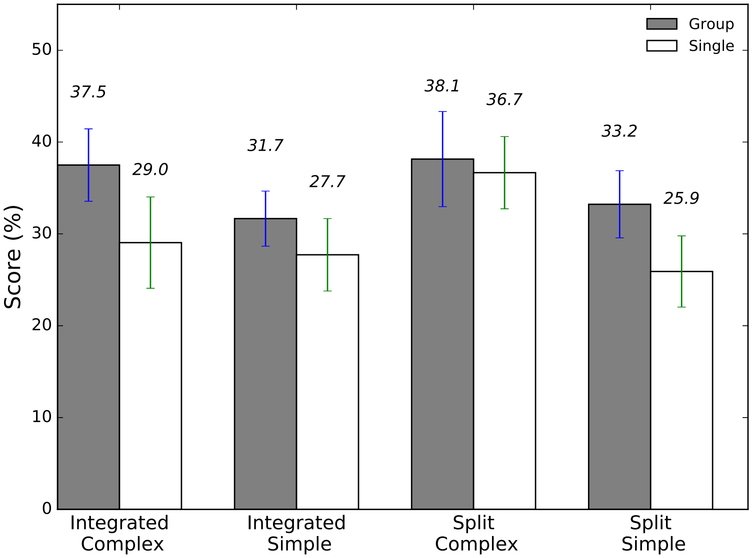


Figure 7. Transfer performances for the toilet task. Error bars indicate standard errors of the mean.

Source	Variable	$\bar{\Delta}$	$F(1,199)$	p-value	η_p^2
Social Context	Transfer	7.81 ± 2.62	8.897	**.003**	.043
	Recall	3.98 ± 2.31	2.981	.086	.015
	Label	1.64 ± 2.79	.345	.558	.002
Difficulty	Transfer	5.42 ± 2.59	4.383	**.038**	.022
	Recall	3.57 ± 2.28	2.457	.119	.012
	Label	3.37 ± 2.76	1.485	.224	.007
Material Design	Transfer	-2.99 ± 3.68	1.335	.249	.007
	Recall	0.39 ± 2.28	.029	.866	.000
	Label	-1.26 ± 2.76	.206	.650	.001

Table 2

Univariate statistical results for the toilet task. ($\bar{\Delta}$) denotes the mean difference between levels (group − single, complex − simple, integrated − split) and the respective standard error.

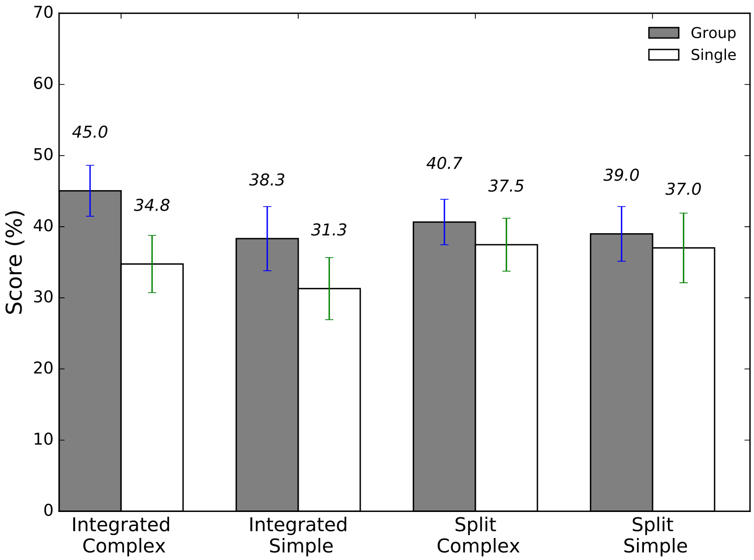


Figure 8. Recall performances for the toilet task. Error bars indicate standard errors of the mean.

participants against the size of the group the respective participants were in (see Fig. 11). The regressions indicated that there was a marginally significant effect for the toilet task, where participants in bigger groups obtained lower scores than those in smaller groups ($\beta = -0.78, 95\% \, C.I.\,[-1.69; 0.14]; t(111) = -1.687, p = 0.094$). However, there was not such tendency for the heart task learning scores ($\beta = -0.25, 95\% C.I.[-1.69; 1.19]; t(111) = -0.342, p = 0.733$). It is worth noting that the differences between the simple and complex conditions were more pronounced in the heart task than in the toilet task and, therefore, that can increase the variability of the data.

4. Discussion

The results showed that the participants in the group condition obtained better learning performances than those in the single condition. Interestingly, this improvement in performance was obtained by individuals working in computer-based learning tasks who did not cooperate nor compete with each other: the effect was only due to the presence of other students completing the same tasks at the same time. Multivariate analyses showed that the presence of other students enhanced learning performances in both the toilet and the heart tasks. Univariate analyses specifically revealed a facilitatory effect of social presence

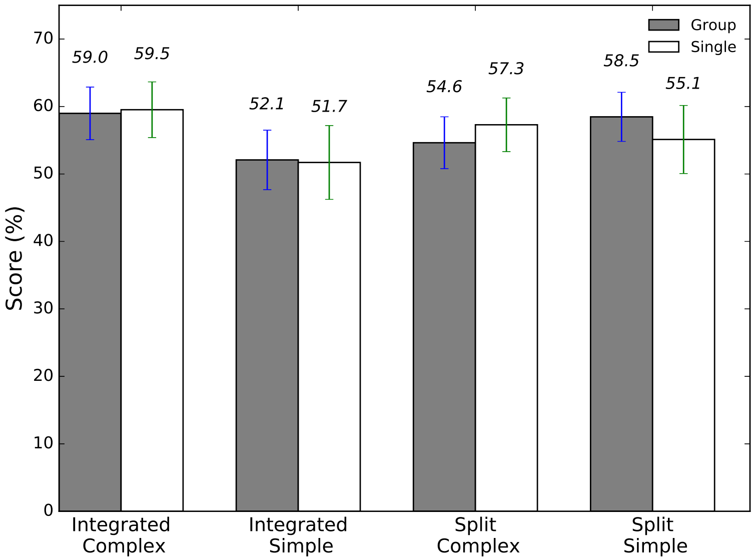


Figure 9. Labeling performances for the toilet task. Error bars indicate standard errors of the mean.

on transfer performances in both tasks. Retention performance was only facilitated in the heart task, but in line with this result there was a tendency ($p = .086$) for better scores in the group condition. The results have implication not only for classrooms but for any setting where individuals work in computers under social presence, such as open offices environments.

There are currently different hypotheses of why social presence can enhance performance, but the root causes of what mediates these effects are still discussed (see Guerin, 2010; Paulus, 2015 for reviews). Some theories propose that the presence of other people can be regarded as a source of stress that ultimately affects the attentional capacity of the individuals (Baron, 1986; Chajut & Algom, 2003; Huguet et al., 1999). In the distraction-conflict theory, Baron and Sanders (1986) propose that social presence can focus attention and have a positive effect in performance on simple tasks. More recently, Chajut and Algom (2003) proposed a theory of attention control which states that factors such as social presence (or time constraints) are stressors that focus one's available attentional resources. The interesting consequence is that this can reduce resources allocated to task-irrelevant clues, enhancing performance. So, paradoxically, social presence may also help focusing attention to the important parts of the learning task. The attentional hypothesis is supported by

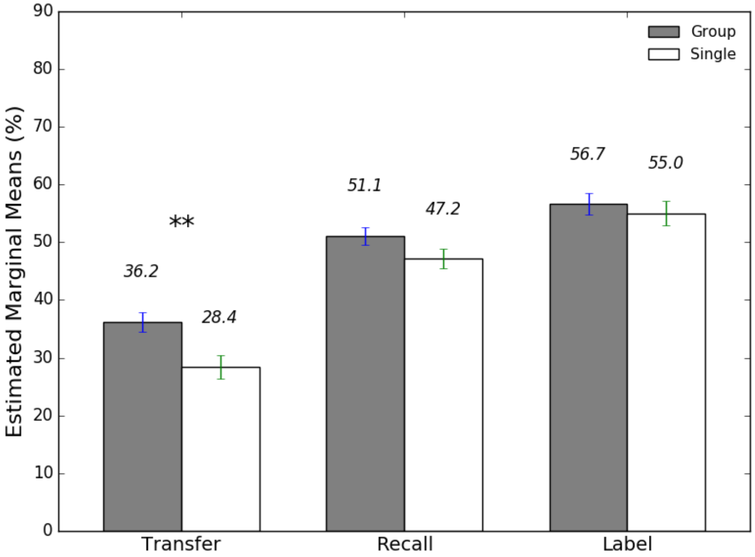
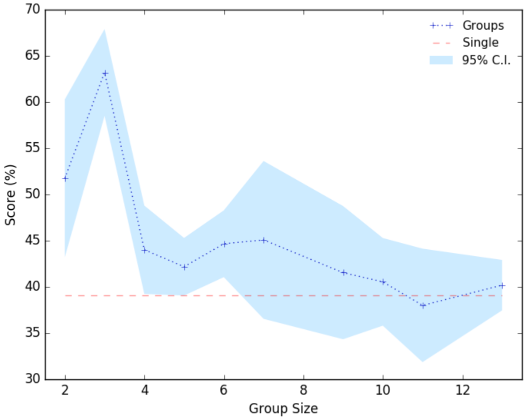


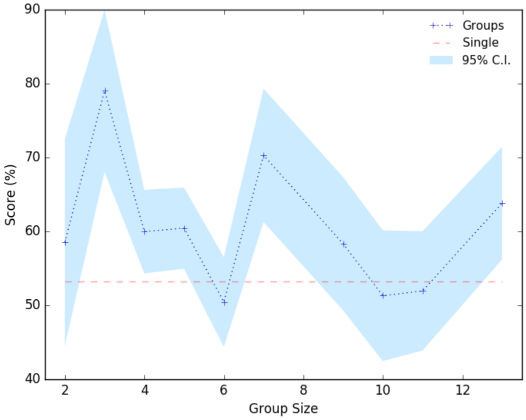
Figure 10. Effect of social context on transfer, recall and labeling scores for the toilet task. Error bars represent standard errors. (**) denotes $p < 0.01$.

studies showing that attention-related brain areas are activated by a person's sheer presence (Monfardini et al., 2016; Verbeke, Pozharliev, Van Strien, Belschak, & Bagozzi, 2014), as well as that the emotional state mediates the focusing of attention (van Steenbergen, Band, & Hommel, 2011). A recent study (Oliva et al., 2017) showed that attentionally mediated eye movements were slower under social presence compared to automatic eye movements, supporting the hypothesis that processes that relay on attention control are affected under social presence.

In order to test the attentional hypothesis of social effects, we varied the task's complexity to see whether these factors would interact with the social condition. Initially, we expected social presence to have a facilitatory effect in performance, particularly in the simple condition in comparison to the complex one. This interaction hypothesis arose from previous research showing that social presence can have divergent effects in performance, where responses in simple and complex cognitive tasks tend to be respectively facilitated and inhibited. Instead, here we report a facilitation effect across conditions regardless of task difficulty. This widespread facilitation observed in the current study is, then, partially in line with the attentional hypothesis of social influences. The lack of performance inhibition should not invalidate the attentional hypothesis. For instance, it could be the case that



(a) Effect of group size on the toilet task.



(b) Effect of group size on the heart task

Figure 11. Effect of the group size. The scores of each post-test were combined to calculate the total score for the toilet (a) and heart (b) tasks. The horizontal line represents the average score of the single condition. The shadowed area represents the 95% confidence interval.

the complex condition was still relatively simple for the participants. Although we piloted the complexity of the tasks (data not shown), the participants might sill have had enough spare capacity to cope with both the task and the added load coming from the social environment. It is clearly stated in the cognitive load field that, as long as cognitive resources are not depleted, the effect of extraneous or extrinsic load may not have a significant impact on learning. Anyhow, this theoretical divergence should not shadow the fact that the mere presence of other co-learners had a significant effect in learning performances. Below, we also discuss alternative explanations for social effects that have been proposed along the years.

Zajonc (1965) was, indeed, the first author to come up with a theoretical framework that accounted for social effects. In his activation theory, Zajonc suggested that social presence increases arousal and alertness on individuals, which eventually can increase performance in a variety of cognitive and physical tasks. Zajonc's hypothesis is related to the Yerkes-Dodson's law, which proposes that every task requires an optimal level of arousal and, in that, social presence may help achieve optimal levels of activation for certain tasks. Other authors proposed later that this arousal activation by social presence can occur especially when the context allows to engage in social comparison (Sanders et al., 1978). In such a case, arousal would increase because students may become more concerned about their own performance in comparison to a social standard. In fact, Cottrell, Wack, Sekerak, and Rittle (1968) suggested that social effects should occur only in situations where individuals can be evaluated. In this same line, a more recent study reported that personality traits such as evaluation apprehension (and extroversion) also moderated the extent at which social presence influenced an individual (Uziel, 2007). This suggests that, probably, the effect of the social context may affect students in different ways depending on individual differences, and whereas some may be benefited by learning in groups, others might prefer solitary conditions. A meta-analysis (Bond & Titus, 1983) concluded that the mere presence of others is sufficient to elicit social influences, and that an evaluation context is not a necessary requirement in order to observe social facilitation-inhibition.

Another important factor that can affect learning when other people are present is cognitive distraction and divided attention. If the number of people in the environment increases, more potential distraction is likely to occur because of inevitable disturbances. To avoid cognitive distraction participants in our study were asked to complete the experiments in silence and to avoid to distract others. However, there are always inevitable noises such as when participants type in the keyboards, eventual coughing, etc, that cannot be avoided. It is probable that with bigger group sizes, these distractive events become more frequent and begin to impair learning. This relationship between group size and performance is probably reflected by the negative correlation between group size and learning performances depicted by the linear regressions (see Fig. 11). Although the regressions did not show a significant effect, they reveal that bigger group sizes may continue affecting learning negatively.

The influence of group size could also be related to social loafing effects. When groups are smaller, individuals may be more aware about their own performance and attitudes because their actions and outcomes are more salient when the focus is put on a smaller group. However, as the number of students in a classroom increases, their individual presence becomes more diluted, and–in a way–concerns about their own performance may decrease. Therefore, the effect of group size should definitely receive more attention to investigate whether there are optimal group sizes that foster learning and, furthermore, at which size groups may become negative for students.

The results also indicated that there was no performance difference between the students that received integrated and split materials. Integrated material layouts tend to enhance learning compared to split designs, allegedly because presenting the information in a more integrated fashion would reduce cognitive resources required for integrating the pictorial and verbal information. However, it is not always the case that integrated designs improve performances compared to split layouts (Jarodzka, Janssen, Kirschner, & Erkens, 2014; Mayer, Heiser, & Lonn, 2001). Our results indicated there was no interaction between the type of social context and the type of instructional design used in the experiment. Probably the reason for this also that participants were successfully able to cope with the added difficulty. However, these hypotheses should be further explored with tasks where the instructional design higher attentional demands on participants.

Here we showed that a simple social manipulation can significantly influence learning performances, and that this effect may be moderated by the size of the group. Given the design of our study, it was not possible to discern whether the effect of the social context is affecting the learning or the evaluation phase (or both). In that, future studies should differentially assess the effect of the social environment.

The present results open new avenues for the study of social interaction through computers. Here we showed that the simple presence of others influenced task performance in a computer-based task even though we gave participants no interaction instructions. The current use of computers easily allows a group of individuals to cooperate and work online on a common task. Thus, future studies should extend the results presented here and assess how performance is affected when, indeed, participants are instructed to cooperate (or compete) with each other. In this, it should important to elucidate how to foster social interactions through computers systems that improve performance and individual wellbeing.

5. Conclusion

The present study explored how the social context can influence individual learning in comparison to when students perform in solitary. The study was performed in a digital classroom where each of the students completed computer-based learning and evaluation sessions. Interestingly, the study revealed that mere presence of other learners had a facilitatory effect on learning performances. The results are consistent with previous research in social facilitation assessed with different cognitive tasks. The results raises the question whether more focus should be given to the varied social environments where students usually perform. In addition, the results also opens new research avenues to investigate the effect of group size and whether different group sizes may have an optimal influence on students.

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Paper III

Pupil dilation reflects the time course of emotion recognition in human vocalizations

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ABSTRACT

The processing of emotional signals usually causes an increase in pupil size, and this effect has been largely attributed to autonomic arousal prompted by the stimuli. Additionally, changes in pupil size were associated with decision making during non-emotional perceptual tasks. Therefore, in this study we investigated the relationship between pupil size fluctuations and the process of emotion recognition. Participants heard human nonverbal vocalizations (e.g., laughing, crying) and indicated the emotional state of the speakers as soon as they had identified it. The results showed that during emotion recognition, the time course of pupil response was driven by the decision-making process. In particular, peak pupil dilation betrayed the time of emotional selection. In addition, pupil response revealed properties of the decisions, such as the perceived emotional valence and the confidence in the assessment. Because pupil dilation (under isoluminance conditions) is almost exclusively promoted by norepinephrine (NE) release from the locus coeruleus (LC), the results suggest an important role of the LC-NE system during emotion processing.

Introduction

Imagine that you hear someone yelling in pain, or laughing: these emotional vocalizations may often carry no linguistic content, yet they convey immediate information about the emotional state of the speaker. When individuals are exposed to affective signals such as nonverbal emotional vocalizations, their pupils usually increase in size as the stimuli are perceived. These pupillary responses were therefore described as reflecting autonomic arousal triggered by emotional stimuli[1,2]. On the other hand, changes in pupil size are known to be linked to cognitive processing[3,4] during tasks that do not involve emotional stimuli. Because recent evidence suggests that emotion processing recruits cortical regions normally associated with cognition[5–7], in this study we investigate whether pupil responses can be used to betray the underlying process of affective processing.

Previous studies report that emotionally arousing stimuli, both auditory and visual, trigger bigger increases in pupil size than emotionally neutral stimuli[1,2,8]. Within emotional stimuli, some authors[9,10] found that negatively valenced stimuli (e.g., crying) trigger larger pupil dilations than positive stimuli (e.g., laughter), whereas others found that both positive and negative stimuli could generate equally large pupil responses[1,2]. Despite some discrepancies, this evidence led to interpret pupillary responses as autonomic reactions elicited by arousing stimuli[1,2] rather than as a reflection of cognitive, emotional processing. This view is supported by findings showing that pupil dilation correlates with measures of arousal such as skin conductance[2], and that stimuli portraying sexual content trigger especially large pupil responses[11,12]. However, emotional vocalizations are perceptual stimuli that require sensory integration in order to be decoded[7,13–15], which may make it cognitively demanding to identify the emotional state of the speaker.

Apart from emotional stimuli, cognitively effortful tasks have long been known to influence pupil size[16]. Accumulating evidence shows that, under isoluminance conditions, changes in pupil size can be attributed almost exclusively to noradrenaline (NE) release from the locus coeruleus (LC)[17]. The LC is the main noradrenergic nucleus in the brain, which sends projections to several cortical regions. The LC is thus believed to exert wide brain modulation of behavioral decisions[3,4]. In addition, recent studies point out a correlated activity between noradrenergic and cholinergic activity in regulating neural states such as alertness[18]. This cholinergic activity was also shown to influence pupil dilation[19]. The link between neuromodulatory activity and pupil size allowed other studies to show associations between pupil dilation and performance in attentional tasks[20], visual discrimination[21], and the speed of visual perceptual choices[22]. For instance, a study reported that pupil dilation predicted the stability of decisions under perceptual rivalry[23].

Perceptual decisions require the accumulation and integration of noisy sensory information, and therefore perceptual decisions usually develop gradually[24,25]. In a similar vein, people exposed to emotional vocalizations may entertain several possible interpretations of the emotional state of the speaker[26]. There is evidence that different brain regions process auditory emotional stimuli in a hierarchical fashion[6,14,27]. The listeners may then need to accumulate perceptual information in order to reach a decision about the emotion portrayed by the stimulus[7,13,15]. The processing of affective stimuli was first thought to be mediated by subcortical regions such as the amygdala. However, recent studies show that cortical areas have a more important role in emotion processing than it was previously thought[6,28]. In fact, current views of affective processing propose a dynamic interaction between cognitive and emotional areas that challenge functional boundaries[29,30]. As the perception of emotional states seems to depend on interactions between cortico-emotional regions, we expect that pupil dilation should reflect both dimensions of emotion processing.

We investigate whether pupil responses reflect cognitive mechanisms of affective processing (in addition to simple autonomic responses to arousing stimuli as previously reported). For this purpose, participants were exposed to naturalistic human vocalizations while they were eye-tracked under isoluminance conditions. In order to analyze the emotion selection process, participants were asked to indicate the moment when they had identified the emotional state of the speakers producing the vocalizations. Later, participants reported the perceived emotional valence of the vocalization and the confidence in their own assessment. We analyzed these data in order to ascertain whether the emotional selection process could be traced through changes in the pupil size of the listeners. Results suggest that pupil responses reflect the time course of affective processing, and that the intensity of perceived emotion only enhances pupil dilation, without being its main driver. We show that pupil dilations are not simply the product of emotional responses, but a rich source of information about affective processing, which opens new avenues for emotion processing research.

Results

Valence and confidence ratings

In order to separate the contribution of affective and cognitive processes to pupil response, we aimed to test stimuli that varied in terms of the valence (positive / negative / neutral), intensity, and ease of recognition of the expressed emotion. As shown in Figure 1, sounds of amusement and sadness offered unambiguous examples of highly positive and negative stimuli, respectively. For neutral stimuli, the valence of both perceived and induced emotion was close to zero (induced valence was estimated based on how participants rated their own emotional experience upon hearing the sound, rather than the experience of the speaker, see Methods for details). The remaining categories covered a wide range of positive, negative, and nearly neutral ratings, often with low confidence. Duration also varied both within and across emotional categories (Fig. 1). We therefore succeeded in developing an array of test sounds that varied in duration, valence, intensity, and ease of identification. This allowed us to assess the independent effects of all these factors on pupil response.

Peak pupil response

We hypothesized that peak pupil response, defined as maximum post-presentation pupil dilation compared to baseline, would be greater for sounds with both very positive and very negative valence compared to relatively neutral sounds. Controlling for confidence, duration and response time, the pupil response did not depend on whether the perceived valence was positive or negative ($L = 0.9$, $df = 1$, $p = .34$). Similarly, the arrow key that participants pressed to indicate readiness to rate the sound (left = negative, right = positive) did not predict the size of peak pupil dilation ($L = 1.6$, $df = 1$, $p = .21$). In contrast, the absolute distance of perceived valence ratings from the neutral point in the middle of the scale, which we hereafter refer to as "valence intensity", was a significant predictor of peak pupil response even after accounting for confidence, sound duration, and response time ($L = 11.7$, $df = 1$, $p < .001$). There was no interaction between valence intensity and its positive or negative "sign" as predictors of pupil response ($L = 0.03$, $df = 1$, $p = .85$). The pupil therefore responded to emotionally charged sounds in general, regardless of whether they were perceived as expressing positive or negative emotional states.

We obtained similar results using ratings of induced rather than perceived valence (not shown). The ratings of perceived and induced valence were highly correlated (r = .81), so in the rest of analyses we focus on perceived valence. Gender and age of participants had no effect on peak pupil response ($L < .9$, $p > .3$ for both). In contrast, the effects of valence intensity, confidence, sound duration, and response time were statistically significant when included in the same multiple regression model ($L > 10$, $p < .002$ for each; see Table 1). The effect sizes were rather small, however. Controlling for confidence, sound duration, and response time, the pupil is predicted to dilate by an extra 1.8% (95% CI [0.8, 2.9]) in response to sounds of maximal vs. neutral valence intensity. The effect of increasing confidence from 0% to 100%, again controlling for the other variables in the model, is to attenuate pupil response by -1.9% (95% CI [-3.1, -0.7], Figure 2). According to the same model, pupil response was also enhanced by 0.8% [0.6, 1.1] for every additional second of sound duration and by 0.5% [0.3, 0.7] for every second of deliberation prior to pressing the response button. Over the observed range of sound duration (0.5 to 6 s) and response times (0.6 to 9 s) these two predictors thus affect pupil response more powerfully than do ratings of confidence and emotion intensity.

In addition to peak pupil response, we also investigated its timing, namely the time from audio onset to peak pupil dilation. The effects of the four main predictors on peak time were consistent with their effects on peak height (compare the two panels in Table 1). The peak of pupil response was delayed in proportion to valence intensity (10.5% [0, 22.1] later peak for maximum versus neutral), sound duration (6.5% [4.4, 8.8] later peak for each second of audio), and response time (13.1% [10.6, 15.5]

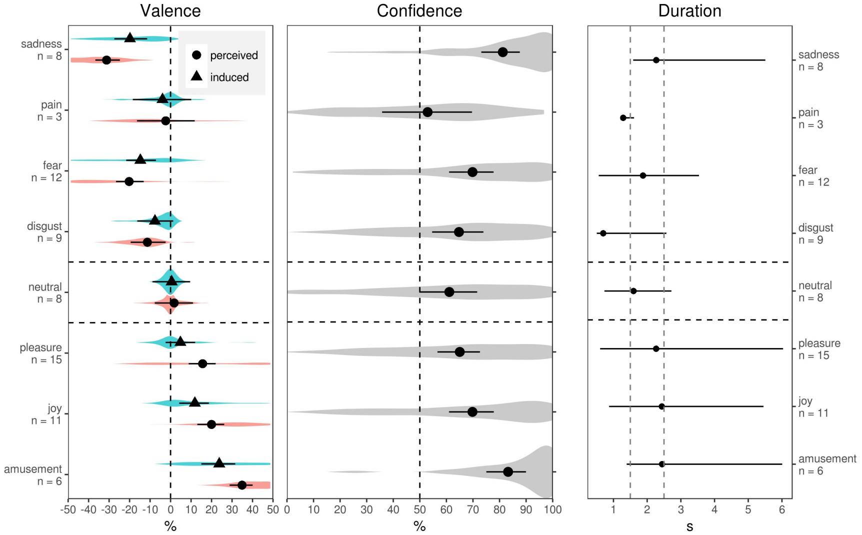


Figure 1. Valence of perceived and induced emotion, confidence ratings, and sound duration averaged per emotion category. Shown: median fitted value with 95% CI overlaid with the distribution of answers for subjective ratings, median with range for sound duration. The region of greatest overlap in sound duration across emotions (1.5 to 2.5 s) is marked with dotted lines. The number of sounds in each category is listed underneath emotion labels.

later peak for each second of deliberation). In contrast, higher confidence predicted an earlier peak (18.1% [0.0, 25.9] earlier for very high versus very low confidence).

To summarize, the pupil responded more vigorously to auditory stimuli of higher emotional intensity, longer duration, and higher ambiguity (measured by slower responses and lower confidence in the nature of perceived emotion). This suggests that both affective processing and cognitive load make independent contributions to pupil dilation.

	Peak Pupil Dilation		**Log-time of peak dilation**	
	β-coeff	95% CI	β-coeff	95% CI
Intercept	9.81	[8.4, 11.2]	0.585	[0.471, 0.700]
Valence Intensity	0.04	[0.02, 0.06]	0.002	[0.000, 0.004]
Confidence	-0.02	[-0.03, -0.01]	-0.002	[-0.003, 0.000]
Sound Duration	0.83	[0.6, 1.1]	0.063	[0.043, 0.084]
Response Time	0.48	[0.3, 0.7]	0.123	[0.101, 0.144]

Table 1. Predictors of peak pupil dilation and its timing. Beta-coefficients in linear mixed-effects regression: the median of posterior distribution and 95% credible intervals.

Pupil response curves time-locked to sound onset

In the previous section we focused on two commonly analyzed characteristics of pupil response curves, namely the size and timing of peak pupil dilation compared to baseline. However, it may also be fruitful to analyze pupil response curves over their entire duration in order to see how they are affected by different characteristics of the auditory stimuli. For this analysis, we time-locked pupil response curves to one of two events: audio onset or pressing the response key. We begin by presenting the

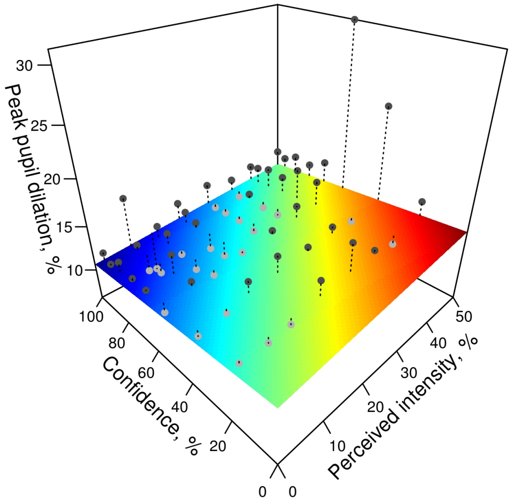


Figure 2. The effect of perceived valence intensity of the caller's emotion (0 = neutral, 50 = maximally positive or maximally negative) and the rater's confidence on peak pupil dilation. The points show raw data aggregated into 8 x 8 quantile bins. The regression plane shows the predicted peak pupil response for a sound of median duration and median response time.

results for time-locking to audio onset (the moment when the sound started playing).

As shown in Figure 3, the pupil began to respond within a few hundred milliseconds of audio onset and continued to dilate rapidly for about one second, regardless of which stimulus was presented. After that pupil responses began to diverge: for neutral sounds (valence close to 50%) peak response was attenuated and shortened compared to sounds of either positive or negative valence. However, sound duration is a confound, since positive vocalizations were on average about 1 s longer than negative and 1.3 s longer than neutral sounds (Table 1). Multiple regression analysis in the previous section allowed us to tease apart the independent effects of duration and valence intensity on peak pupil response, but it is not so straightforward to adjust for duration when analyzing entire pupil response curves. As a first approximation, we extracted response curves for those 25 out of 72 sounds that were relatively similar in duration (between 1.5 s and 2.5 s, see Fig. 3, thus standardizing stimulus duration while preserving sounds from all emotional categories. For these shorter stimuli, the height of peak response still depended on valence intensity, albeit at a trend level: $L = 3.1$, $df = 1$, $p = 0.079$ (cf. for all 72 sounds: $L = 11.7$, $df = 1$, $p < .001$), and peak pupil dilation was similar for positive and negative sounds: $L = 1.8$, $df = 1$, $p = .18$ (cf. for all 72 sounds: $L = 2.1$, $df = 1$, $p = .15$). The main difference compared to time curves for all sounds was that the temporal characteristics of pupil response (time of peak dilation, rate of initial dilation and post-peak contraction) were less dependent on the absolute valence of perceived emotion (Figure 3).

The analysis of complete pupil response curves time-locked to stimulus onset thus suggests that the time course of pupil dilation depends strongly on the duration of stimulus, while peak dilation provides an excellent summary of overall pupil response.

Pupil response curves time-locked to response

Pupil response curves can also be time-locked to the moment when the participant pressed one of the two response keys - left for negative, right for positive - indicating readiness to rate the caller's emotion. As shown in Figures 4 and 5, the moment of response slightly preceded peak pupil dilation: the average time from pressing the response key to reaching maximum pupil dilation was 0.37 ± 1.7 s (M ± SD). Participants tended to respond 1-2 s after sound offset if the sound was very short, whereas for sounds longer than about 3 s they tended to respond while the sound was still playing, with a lot of individual variation (see Supplementary material online, Figure S1). Interestingly, even though participants responded more slowly to longer sounds (effect of duration on arrow response time: $L = 21.2$, $df = 1$, $p < .001$), sound duration had no effect on the lag between peak pupil dilation and pressing the response button ($L = 0.06$, $df = 1$, $p = .81$). Figure 5 suggests that this lag is more pronounced for both very negative and very positive sounds compared to neutral sounds. This is confirmed by regression analysis: both the absolute valence of perceived emotion and confidence are independent positive predictors of the lag between peak pupil response and pressing the response key ($L = 3.9$ and 4.7, $p = .05$ and .03, respectively, $df = 1$ for both). However, this effect is both uncertain and relatively weak: the time from response to peak pupil dilation is predicted to be 280 ms greater (95% CI [10, 550]) for sounds of maximal vs. neutral valence intensity and 360 ms greater (95% CI [38, 689]) for high vs. low confidence. This indicates that lower cognitive effort and higher perceived emotional intensity push peak pupil response slightly beyond the moment of decision making.

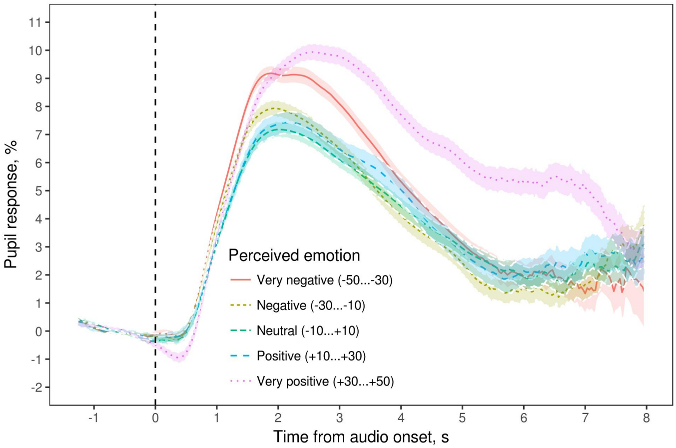
To summarize, peak pupil response was delayed and enhanced for longer versus shorter sounds, but it still closely coincided with the moment when a participant made up their mind about the nature of portrayed emotion and pressed the response key (see Figs. 4 and 5). This also speaks in favor of analyzing pupil response curves time-locked to response, rather than to onset of stimulus presentation, since this allows us to abstract from stimulus duration.

Discussion

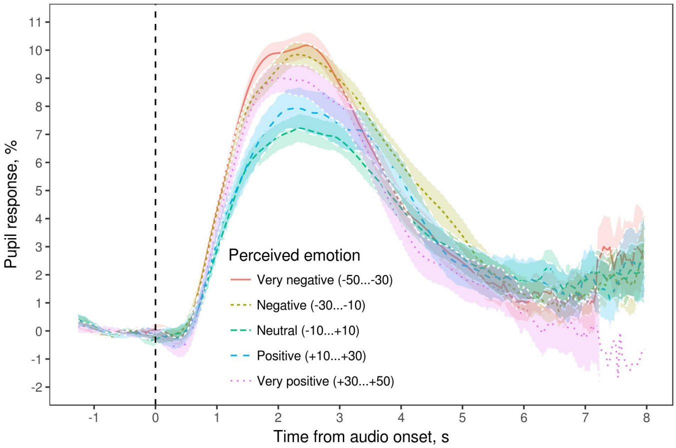
In the present study we measured pupil responses while participants formed decisions about the emotional state of speakers. For this purpose we used nonverbal vocalizations that portrayed several emotional states of varying intensity and ambiguity[26]. This investigation is the first to show that pupil responses to emotional charged stimuli are temporally aligned with decision making about the nature of the speaker's emotion. Additionally, the results indicate that pupil dilation predicts properties associated with the listeners' choices, such as the perceived emotional valence of the stimulus and the confidence level in their own judgment. Specifically, peak pupil responses were larger for stimuli rated with high valence and when the listener was less confident about the stimulus valence. Thus, we demonstrate that cognitive and emotional factors make independent contributions to pupil response within a single emotion recognition task.

This is also the first study that assessed pupil responses to naturalistic emotional vocalizations, recorded in real-life situations, associated with a wide range of affective states, and varying in valence, intensity, ambiguity, and duration[26]. In line with previous reports[1,8], we found that the perceived emotional valence of the sound caused larger pupil dilations in comparison to sounds perceived as neutral. However, the emotional valence seemed to have only a minor contribution to the overall pupillary response. Emotionally salient sounds did trigger larger dilations, but this effect was relatively low (2%) in comparison to both the overall pupil responses (10%) and the effect of sound duration and response time (∼3-5%). In addition, sounds perceived as neutral also triggered pupil responses that significantly separated from baseline (see Figure 4), indicating that pupil dilation did not exclusively depend on the perceived emotional valence. In contrast, pupil fluctuations seemed to follow the decision formation about the emotional state of the speaker. In particular, the pupil size started to respond shortly after audio onset and continued to dilate throughout the emotional state selection process. This sustained increase in pupil size continued until just after the decision about the emotional valence was made, following which pupil size returned to baseline levels (see Figures 4 and 5). Such pupillary behavior was consistently robust across a wide range of stimuli that varied in emotional valence, ambiguity, and duration. Taken altogether, the results indicate that the time course of pupil response betrays the perceptual process of selecting the emotional state of the speaker, whereas the perceived emotional valence intensity remains only as a moderator of the response.

Current views of visual perceptual decision making propose that when there is a need to select one of several competing perceptual options, individuals must accumulate and integrate perceptual evidence in order to select between alternatives[24,31]. In a similar fashion, the decoding of nonverbal vocalizations is not always a perceptually trivial task, and vocalizations can often be interpreted in different ways. Naturalistic vocalizations can be very intense, but inherently more ambiguous than actor portrayals of particular emotions, which are intended to be maximally transparent[26]. This reduced correlation between emotional intensity and ease of recognition allowed us to disentangle their independent effects on pupil response. We propose that the sustained increase in pupil dilation at the beginning of trials reflects this period in which perceptual evidence is decoded



(a) Aggregated pupil response for all 72 sounds.



(b) Aggregated pupil response for a subset of 25 sounds
with duration between 1.5 and 2.5 s

Figure 3. Aggregated pupil responses for all sounds (a) and for a subset of stimuli of similar duration (b). The dashed line at 0 s represents the moment where sounds started. As expected, emotionally charged sounds triggered larger pupil dilations in comparison to neutral sounds. Shaded areas represent standard errors for each time point.

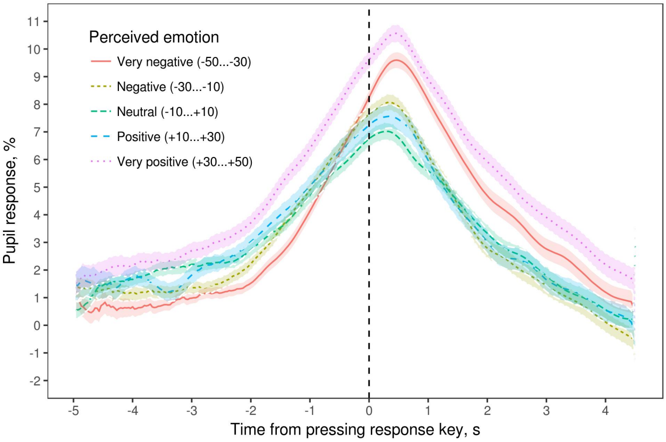


Figure 4. Pupil curves time-locked to response times. The dashed line represents the moment participants responded about the emotional valence of the stimulus. Pupil size increased throughout the emotional selection process until just after participants identified the emotional valence of the stimuli. This pattern was consistent across a wide range of stimuli that varied in emotional valence, valence intensity and duration.

and integrated in order to decide between competing perceptual alternatives, which demands cognitive resources. As sufficient information is gathered, individuals can select the most likely emotional state of the speaker. After a selection is made, there is no need to sustain high cognitive engagement in processing the vocalizations, which in turn leads to a decrease in pupil size. In this process, vocalizations perceived as ambiguous demand more cognitive resources and take more time before they are fully decoded, which translates into larger pupil dilations. In support of this interpretation, we observed that peak pupil dilation was delayed and enhanced when the confidence ratings were low.

There is still disagreement about whether positive and negative stimuli trigger equally large pupil responses. Whereas some studies reported that negatively valenced emotions trigger larger pupil dilations than positively valenced ones[9,10], some others found that both positive and negative stimuli can trigger equally large dilations[1]. In line with the latter view, we found that the emotional modulation of the pupil response was independent of whether the stimuli were perceived as positive or negative. The peak amplitude of pupil responses was better predicted by the stimulus valence intensity than its valence (positive or negative). In other words, both positive and negative emotional stimuli were capable of causing equally large pupil responses; however, the more a stimulus deviated from an emotionally neutral sound, the more pupil dilation it elicited.

Although the mechanisms of auditory emotional processing are not fully understood, recent studies propose that these emotional signals are processed in a multi-step, hierarchical fashion, involving both subcortical (e.g., amygdala) and cortical regions (e.g., prefrontal cortex)[6,7]. Brain structures were normally functionally separated into areas that process emotion (e.g., the amygdala) and those related to cognition (e.g., prefrontal cortex). However, recent evidence challenge the idea of division between emotion and cognition as excluded from each other. Different studies demonstrate that, for instance, cortical areas show activation patterns to emotional stimuli that are as, or even more, consistent as that of the amygdala[6,27]. Conversely, arousal responses are equally critical for cognitive functions[32,33]. For instance, arousal responses that involve the amygdala and the LC are important for memory consolidation[34] and attention[32,33,35,36]. Because we find that pupil size is sensitive to both cognitive and emotional factors, pupil dilation may open new research avenues for the study of cognitive-emotional interactions.

Under isoluminance conditions, pupil dilation primarily reflects noradrenergic[17] and cholinergic neuromodulation[18]. As such, different studies found associations between pupillary responses and mental effort[16], visual perception[21,37] and the speed of visual discrimination tasks[22]. These previous studies, however, used mostly visual tasks that did not include emotional processing. Here we extend such results to perceptual discrimination of affective stimuli, where pupil dilation also reflects the processing of emotional signals. In a schema of cognitive-emotion interplay, our results suggest that the LC, with its high connectivity (e.g., amygdala, prefrontal cortex), emerges as one potential hub that integrates emotional and cognitive inputs

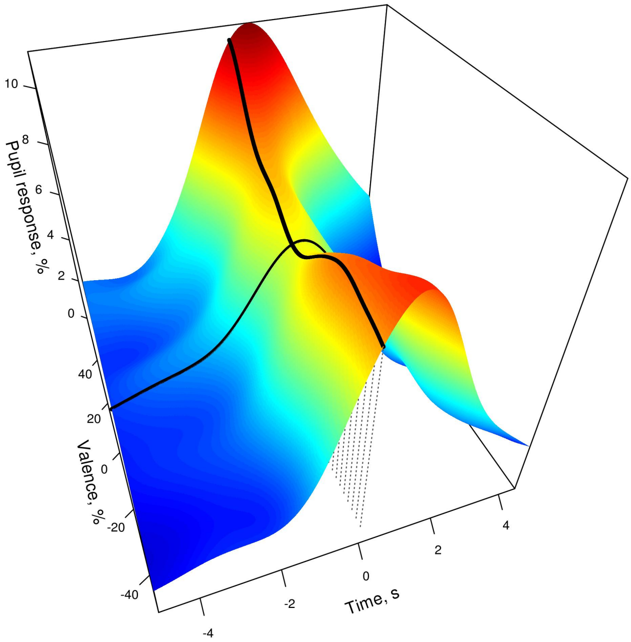


Figure 5. Generalized additive model with a single smooth term for a combination of time and emotion rating. Elevation and color show the size of pupil dilation compared to the baseline. The "valence" coordinate shows the rating of the caller's emotion given after pressing the response key (time 0, marked by the line on top of the ridge): -50 = very negative, 0 = neutral, +50 = very positive. The thin black line traces pupil trajectory for a neutral sound, and the thick black line marks the moment of response.

during affective information processing.

Methods

Participants

Thirty-three university students (mean age = 25 years, SD = 2.8, age range = 21–35 years; 13 men) voluntarily participated in the experiment and received a cinema ticket in return. No participant suffered from significant data loss (see Data Analysis), and all participants were included in the analyses.

Ethics statement

In accordance with the Swedish law (SFS 2003: 460, 16 §), all participants gave written consent for taking the experiment. In accordance with the Swedish Act concerning the ethical review of research involving humans (2003:460), the present study was exempt from the requirement for ethical approval.

Setup

The study was conducted in a room equipped with remote eyetracking systems. The auditory stimuli were presented through headphones connected to a computer and a 22-inch monitor (DELL P2210, 1680 x 1050 at 60 Hz). A viewing distance of approximately 65cm was maintained using chinrests. The pupil diameter of the participant's right eye was measured by a noninvasive infrared "RED-m" (SMI, Teltow, Germany) eye tracker at a rate of 120 Hz. All visual and auditory stimuli were presented using Psychopy[38] (Version 2.85) and SMI iView X (2.8.43).

Stimuli

Experimental stimuli consisted of 72 sounds, including 68 authentic emotional non-linguistic vocalizations from a validated corpus[26] and four neutral stimuli from Montreal Affective Voices[39] (MAV). The neutral sounds from MAV contained a single vowel [a] pronounced with a flat intonation. The authentic emotional vocalizations consisted of a variety of laughs, screams, moans, grunts, and other sounds obtained from real-life video footage on social media. The accuracy with which particular emotions were recognized by listeners was reported in the original study[26], allowing us to select both unambiguous (n = 36) and ambiguous (n = 32) sounds. We were less interested in the accuracy of discriminating individual emotional states such as pain and disgust, so our selection criterion of ambiguity involved only the accuracy of recognizing the valence as positive or negative in the validation study[26]. We also strove to include sounds of varying intensity in both the ambiguous and the unambiguous groups. In particular, some ambiguous stimuli could be interpreted as either highly positive or highly negative. All sounds were normalized for peak amplitude to standardize their loudness[26].

The main characteristics of experimental stimuli are summarized in Table 2. Emotion categories in the left column correspond to the emotion most commonly perceived by listeners in the validation study[26], rather than to the production context or the "true" underlying emotion of the speaker. Our objective in selecting these stimuli was to include a wide range of sounds that varied in their perceived valence (positive, negative, and neutral), intensity (from mild to extreme, as for uncontrolled sobbing or orgasmic moans), and ease of recognition. We verified that the selected positive and negative vocalizations were not significantly different in terms of intensity ($F(1,62) = 0.05$, $p = .82$) and ease of valence recognition ($F(1,62) = 1.88$, $p = .18$). However, positive vocalizations were approximately 1 s longer compared to negative vocalizations ($F(1,62) = 8.2$, $p = .006$). To account for this difference, we included duration as a covariate in all analyses.

Emotions	N stimuli (M/F)	Valence Recognition (%, M±SD)	Perceived Intensity (%, M±SD)	Duration (S)	Examples
Amusement	6 (2/4)	94 ± 15	58 ± 16	3.4 ± 1.9	Laughs
Joy	11 (4/7)	80 ± 20	40 ± 11	2.5 ± 1.4	Laughs, whoops
Pleasure	15 (8/7)	66 ± 19	49 ± 23	2.8 ± 1.9	Moans, whimpers
Total Positive	**32**	**76 ± 21**	**48 ± 19**	**2.8 ± 1.7**	–
Total Neutral	**8***	**–**	**–**	**1.5 ± 0.7**	–
Disgust	9 (6/3)	86 ± 15	40 ± 20	1.1 ± 0.7	Grunts, sighs
Fear	12 (6/6)	77 ± 26	50 ± 22	1.7 ± 0.9	Screams, roars
Pain	3 (1/2)	50 ± 17	22 ± 6	1.4 ± 0.2	Gasps, whimpers
Sadness	8 (2/6)	94 ± 12	67 ± 15	2.9 ± 1.3	Cries
Total Negative	**32**	**81 ± 22**	**49 ± 23**	**1.8 ± 1.1**	–

Table 2. Description of experimental stimuli (N = 72). The ratings are based on a previous validation study[26]. (*) Four neutral sounds from Belin et al. (2008) and four mild, hard-to-recognize sounds from Anikin & Persson (2017).

Procedure

Participants received a brief oral description of the experiment, and subsequent instructions were all presented on the computer's screen. Participants completed eight practice trials, in which they heard three negative, two neutral and three positive sounds. This allowed participants to familiarize themselves with the range of stimuli that they would later rate. After the practice trials, the eyetrackers were calibrated. After calibration a pre-experiment pupil resting baseline was recorded for 45 s. Participants commenced each trial by looking inside a fixation circle subtending 1.1° at the center of the screen and pressing the upper arrow key to indicate readiness to begin. In order to avoid temporal predictability, the sound stimulus began after a non-ageing foreperiod[40] of 5-11 seconds, where the probability of it terminating per unit of time was constant after 5 seconds and curtailed at 11 s. The relatively long foreperiod provided enough time following each trial for the pupil to subside back to baseline. As the sound stimulus was played, participants first rated the perceived valence of the sound as either positive (right arrow key) or negative (left arrow key); they were instructed to respond as soon as they recognized the emotion of the sound. In order to record the peak pupil response, the eyetracking recording continued for 4.5 s after the participant's manual response.

Participants were instructed to look inside the fixation circle until the end of the trial to ensure no gaze displacement. After this period the fixation circle disappeared, and participants received three questions about the sound stimulus. First, they had to rate the perceived emotional valence of the sound using a continuous rating scale, "Is the person experiencing positive or negative emotions?". This question corresponds with the manual response they had to perform first by pressing one of two arrow keys, except that this time the rating was continuous rather than binary. Secondly, they stated their confidence about their assessment. The valence of induced emotional state was measured by the third question, “How do you feel about the sound? Does it convey positive or negative emotions?”. The inclusion of this subjective report was intended to investigate whether the pupil response related more to the capacity to recognize the emotional state of the speaker or to the subjective experience of the listener. Participants rated each sound on a scale of 0 to 100, where 50 corresponded to a neutral sound. To make the results more intuitive, we present valence ratings on a transformed scaled: -50 = very negative, 0 = neutral, and 50 = very positive.

The experiment used 72 sound stimuli presented in two blocks, each of them containing an equal number of positive and negative sounds. The presentation order of the stimuli was randomized for every participant, and they could take a break before starting with the second block.

Data Analysis

For each trial, baseline pupil diameter was calculated as the average pupil diameter over a period of 1.3 s before the beginning of the trial (at the end of the intertrial foreperiod). Pupil responses were computed as the percentage difference between trial baseline diameter and the peak pupil size measured until 4.5 s after the participant’s response (left/right arrow key press). All pupil dilations were normalized by the pre-experiment resting baseline taken at the beginning of the experiment. Pupil diameter data were pre-processed in Python (2.7.11) to detect and remove blinks and gaze displacement. Trials in which their gaze was displaced from the fixation circle were excluded from the analyses, because it can affect pupil diameter measurement. Periods of blinks were completed using cubic spline interpolation. For computational efficiency, pupil signals were then smoothed using a Savitsky-Golay filter (window = 21, order = 3) and downsampled from 120 Hz to 30 Hz. Trials where blinks and missing data exceeded 20% of the total trial samples were considered invalid and excluded from all analyses. We excluded 5.2% of all trials, preserving on average 68 out of 72 trials per participant (median 70, range 41 to 72). No participants were excluded from the analysis.

All statistical analyses and plotting were performed in R 3.4 (https://www.r-project.org). To analyze the valence and confidence ratings for each emotion, which we recorded on a scale from 0 to 100%, we assumed that the outcome variable followed a beta distribution and applied Bayesian beta regression. The valence of both perceived and induced emotion was analyzed within a single mixed model with an interaction term Emotion x Type of valence (perceived or induced) and two random intercepts: per participant and per stimulus.

The location and height of peak pupil dilation was extracted from the pupil response curve for each trial. It was then analyzed using Gaussian linear mixed models with random intercepts per participant and per stimulus. This allowed us to work with unaggregated trial-level data, while taking into account the variability of pupil response due to differences between participants and between experimental sounds. Statistical significance of predictors was tested with likelihood ratio tests using lme4 package[41]. To extract confidence intervals, we fit analogous Bayesian models, which arguably offer more robust estimates in the context of multilevel regression. All Bayesian models were created in Stan computational framework (http://mc-stan.org/) accessed with brms package[42]. To improve convergence and guard against overfitting[43], we specified mildly informative conservative priors.

Pupil response curves were also analyzed as time series, as follows. Preprocessed curves from each trial were first time-locked to the event of interest (audio onset or pressing the response key). These trial-by-trial curves were then aggregated by perceived valence (in bins) and time from the locking event, and standard errors were calculated for each time point. In addition, we treated valence as a continuous variable and fit a Generalized Additive Model (GAM) from mgcv package[44], specifying a single smoothing term for time and valence. This allowed us to visualize pupil response over time as a function of the perceived valence of the stimulus.

Python and R scripts for data preprocessing and statistical analysis, experimental sounds, and raw data are available in supplementary materials.

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Author contributions statement

M.O. and A.A. conceived the experiment, M.O conducted the experiment, A.A and M.O. analyzed the results. All authors reviewed the manuscript.

Additional information

Competing financial interests The authors declare no competing financial interests.

Paper IV

Pupil size and search efficiency in low and high perceptual load

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The ability to focus on a task while disregarding irrelevant information is an example of selective attention. The perceptual-load hypothesis argues that the occurrence of early or late selection mechanisms is determined by task-relevant perceptual load. Additionally, accumulating evidence shows that pupil size serves as proxy of locus coeruleus-norepinephrine (LC-NE) activity, a system associated with cognitive and attentional mediation. Here, we assessed the influence of pupil size as predictor of load-related early and late selection performance. Participants were asked to search for a target in conditions of high and low perceptual load, while ignoring irrelevant stimuli. In line with the perceptual-load hypothesis, results showed that pupil baseline size, measured prior trial onset, significantly predicted the upcoming search efficiency only in low perceptual load, when selection depends on cognitive control functions. In addition, pupil dilation and its time course reflected response times in both perceptual load conditions, an association that was enhanced in high load. Thus, this study relates early and late selection mechanisms, as defined by the perceptual-load hypothesis, with pupil-related LC-NE activity. The results suggest that the degree with which LC-NE influences behavioral performance is related to the perceptual load of the task at hand.

Introduction

When a person is engaged in studying, playing sports or focused on reading this article, that individual is likely to become simultaneously unaware of events happening in their surrounding. These examples of selective attention occur as the result of processing limitations, where either due to bottom-up or top-down mechanisms, only a limited amount of the information received from the environment is fully processed for meaning.

Perceptual Load and the Locus of Selection

Researchers have been long interested in detecting the locus of selection within the course of information processing. The first influential theory that accounted for selective attention was proposed by Broadbent (1958) and later updated by Treisman (1969). In this theory, they proposed a two stage perceptual mechanism where first, physical features of the stimuli are extracted in parallel and filtered, so that only the stimulus of interest would receive further processing. According to this theory, selection occurs in an early processing stage after which irrelevant stimuli receive no further analysis.

Early selection models resulted well suited to explain selection in perceptually difficult tasks, such as in “shadowing” experiments (Cherry, 1953), which involve high perceptual load (i.e., complex target stimulus, large set size). In these experiments, participants had to hear two different auditory messages played on each ear, and repeat out loud (or to “shadow”) only one of the messages. In line with early selection models, these experiments showed that individuals were good at efficiently selecting one channel while at the same time disregarding the irrelevant one (Treisman, 1969). However, this model failed to explain selection under low perceptual load (i.e., simple target stimulus, small set size). A clear example of the latter are flanker tasks (Eriksen & Eriksen, 1974) where participants are asked to report the presence of one out of two possible targets while at the same time ignoring a peripheral distractor. This paradigm shows that under low load, individuals are unable to ignore irrelevant stimuli, which translates into slower responses compared to when no distractor is present.

Deutsch and Deutsch (1963) would propose a model capable of explaining selection in tasks with low perceptual load, such as the flanker task. In contrast to early selection, this model posits that perception proceeds in parallel across all stimuli. According to this account, selection of the target stimulus occurs "late" in processing, as a result of the need to provide a pertinent behavioral response. Late selection models explain flanker interference effects by predicting that because of the absence of early perceptual filtering, irrelevant stimuli would compete with the target stimulus and influence response times.

These seemingly contradictory differences between models led Kahneman and Treisman (1984) to suggest the existence of two different attentional mechanisms acting in different circumstances, a hypothesis that was further developed in the perceptual load hypothesis (Lavie, 1995; Lavie & Tsal, 1994). The perceptual load model integrates early and late selection accounts by proposing that the perceptual load of the task at hand is the main factor determining whether early or late mechanisms will occur. As in the late account, it proposes that perception is an automatic process, in the sense that it proceeds in parallel across all stimuli without voluntary control. This explains, for instance, why a flanker may interfere with the response to the actual target: in low perceptual load, spare capacity spills over involuntary to irrelevant stimuli. In addition, the perceptual load hypothesis adds that perception proceeds automatically only until the perceptual system runs out of capacity, in which case not all perceptual information receives further processing. By increasing the perceptual load in a flanker task, Lavie and Cox (1997) showed that high perceptual load can prevent the interference produced by a competing flanker. In addition De Fockert, Rees, Frith, and Lavie1 (2001) showed that cortical functions are important for selective attention in conditions of low perceptual load. In such cases, all information is perceived and working memory seems to play a key role in reducing the effect of distractors on task processing by maintaining the prioritization of relevant information. In a series of experiments, it was show that by taxing the participants' working memory, selective attention was impaired in low load but not in high load (De Fockert, 2013; Lavie, Hirst, de Fockert, & Viding, 2004).

Attention and Pupil Size

Recent studies have started to link changes in pupil size with perceptual processes (de Gee, Knapen, & Donner, 2014) and decision making (Einhäuser, Stout, Koch, & Carter, 2008). This relationship arises because under isoluminance conditions, fluctuations in pupil size are largely caused by norepinephrine (NE) release from the locus coeruleus (LC) (Joshi, Li, Kalwani, & Gold, 2016). The LC sends inputs to different brain areas involved in control functions and attentional processing (Foote, Berridge, Adams, & Pineda, 1991; Joshi et al., 2016). As such, the LC-NE system is believed to exert wide brain modulation (Aston-Jones & Cohen, 2005) that enhances signal-to-noise ratio in the processing of sensory input (Arnsten & Rubia, 2012; Mather, Clewett, Sakaki, & Harley, 2015; Sara & Bouret, 2012b) as well as improving cortical representations of perceptual signals (Warren et al., 2016). In particular, the LC-NE system seems to be highly involved in the detection of behaviorally relevant stimuli. For instance, electrophysiological studies in monkeys performing a go/no-go task showed that LC responds only to target stimuli, producing phasic activation bursts that are subsequently followed by pupil dilation (Aston-Jones, Rajkowski, Kubiak, & Alexinsky, 1994; Usher, 1999). In this task, epochs of low LC tonic activity correlated with enhanced attentional performance and pronounced phasic spike bursts in response to target detection. On the contrary, high tonic activity correlated with poorer attentional performance, reflected by slower responses and higher frequency of false positives to the no-go stimuli.

Although accumulating evidence links noradrenergic activity with attention and cognitive processes, the role of LC-NE activity within attentional selection mechanisms is not yet understood.

The Present study

In the present study we examined the relationship between LC-NE activity –as measured by pupil size– and the efficiency of visual search for a target in conditions of high and low perceptual load. For such purpose we adapted a task previously used for the study of perceptual load and selective attention (Lavie, 1995; Lavie & Cox, 1997; Theeuwes, Kramer, & Belopolsky, 2004) so that it could be used under isoluminant conditions. In this task, participants are instructed to report the appearance of a target letter (X or N) within a central search array that contains the target together with other five non-target letters (Figure 1). Simultaneously, participants have to ignore a peripheral distractor. The distractor letter can be compatible (i.e., same as target letter) or incompatible (i.e., alternative target letter). The perceptual load of the task is manipulated by varying the similarity between the target with the non-target letters (Figure 1). In high load, the non-target letters in the array are more similar to the target than in conditions of low load. In this way, perceptual load is manipulated while keeping similar set sizes between the the low and high load search conditions.

As described above, this paradigm predicts that under low load, all stimuli from the search array will receive perceptual resources and analyzed in parallel. This leads to a condition of late selection, where all stimuli access awareness. Selection is then resolved after identification, in which case, cortical functions and working memory become critical for successfully selecting and prioritizing relevant information (De Fockert, 2013; Lavie et al., 2004).

In this context, we expect that visual search efficiency should be modulated by LC-NE activity, and reflected by pupil size, particularly in conditions of low perceptual load. In high perceptual load, in contrast, not all perceptual information is processed at once. This is because of a rather passive mechanism, where perceptual information is filtered out due to capacity limits. In such a case, we expect pupil size not to predict search efficiency.

The perceptual load of the main task will also influence distractor processing. Low perceptual load arrays may allow the perception of the distractor, which may interfere with response selection in the case of incompatible trials. High perceptual load displays, in contrast, will deplete resources and distractor compatibility should have little influence on response times. As such, distractor processing is an indirect measure of perceptual load effect and the occurrence of late and early selection mechanisms.

Methods

Participants. Nineteen participants (mean age = 26, age range = 21-41) with normal or corrected-to-normal vision voluntarily participated in the experiment and received a cinema ticket in return. Data from two participants were discarded due to poor eyetracking data quality (more than 50% of data loss, see Data Analysis).

Ethical Statement. In accordance with the Swedish law (SFS 2003: 460, 16 §) all participants gave written consent for taking the experiment. In accordance with the Swedish Act concerning the ethical review of research involving humans (2003:460), the present study was exempt from the requirement for ethical approval.

Apparatus. The presentation of the stimuli was controlled using Psychopy (Peirce, 2007) (v2.85). The stimuli were presented on a 1280 X 1080 monitor screen (Samsung 931C) with a refresh rate of 60Hz. Pupil size and gaze position were recorded with a tower-mounted eyetracker (SMI, Teltow, Germany) at 500 Hz. Participants used a chinrest and maintained a viewing distance of 65 cm. Isoluminant colors for the letters and the background were approximated using YUV color encoding system and later adjusted to be perceptually isoluminant with the flicker-fusion procedure (Lambert, Wells, & Kean, 2003). The resulting colors had the RGB values of 69, 149, 24 for the background and 223, 61, 61, for the letters. Under these conditions, the luminance was kept constant throughout the experiment at 56 cd/m2.

Stimuli. The target letters that participants were instructed to report were X and N. In the low load condition, the non-target letters were all “O”. In the high load condition, the non-target letters were the letters “W”, “Z”, “F”, “H”, “T”. In this way, there were always 5 non-target letters in both the high and low conditions, however, the processing demands were higher for the high perceptual load condition. Each letter subtended 1.1° in height and 0.8° in width. The letters were presented randomly at 45°, 90°, 135° of arc on an imaginary hexagon at an eccentricity of 3.5°. The distractor letter was presented randomly to the left or right sides of the letters array with a random position varying between +/- 10° of arc. The distractor was displayed at an eccentricity of 4.5° from the fixation point.

Design and Procedure

Participants received 192 experimental trials separated in 4 blocks of 48 trials each with optional breaks in between blocks. Half of the participants started with

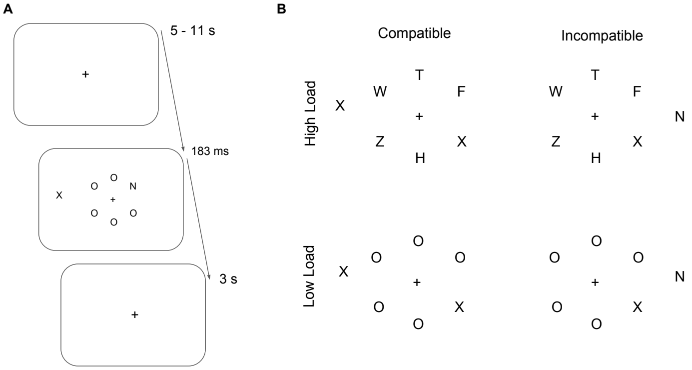

Figure 1. **A**. Participants started fixating at a central cross and after a non-aging foreperiod a search array was presented and participants had to report the target stimulus. **B**. Examples of the search arrays from each condition.

the high-load condition (HLHL); the other half started with the low-load condition (LHLH). There were equal number of compatible and incompatible trials on each block and the position of the distractor was randomized every trial. Participants completed at least 48 practice trials. If necessary, the practice session was extended until participants reached at least 70% of correct trials on each load conditions. After calibration of the eye-tracker, a resting state baseline diameter was calculated as the average pupil diameter during 45 s of passive fixation. The experimental trials began with the presentation of a fixation cross at the center of the screen, which was presented following a non-ageing foreperiod of 5-11 s. A non-ageing foreperiod reduces the effect of target onset expectations (Oswal et al., 2007). The relatively long foreperiod allowed the pupil to subside back to baseline levels. Subsequently, the central search array and distractor were displayed for 183 msec (see Figure 1. The short presentation time was to avoid the use of eye movements for the visual search. If an X was presented, the participants had to press the “2” key; if an N was presented, the observers pressed the “0” key. Participants were instructed to report the target present in the central search array and to ignore the peripheral distractor. Feedback about their performance (response times and error rates) was provided after the completion of each block.

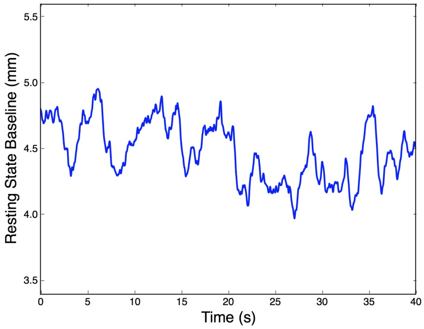

Figure 2. Pupil size fluctuations during passive fixation. Spontaneous changes in pupil size correlate with to LC-NE activity (Joshi et al., 2016). An average resting state baseline was extracted from each participant in order to normalize pupil size.

Data Analyses. The baseline diameter for each trial was calculated as the average diameter over a period of 1 s before trial onset (during the inter-trial foreperiod). Pupil responses were computed as the percentage difference between the trial baseline and the peak pupil dilation measured measured until 3 s after the participant’s key press. Pupil data were processed in Python (2.7.11) to detect blinks and gaze displacement. Trials containing blinks between trial onset and the peak dilation and/or when gaze was displaced more than 1.2° from the central fixation cross were excluded from all analyses. Trials in which periods of blinks, missing data and gaze displacement represented more than 20% of the total trial samples were also excluded. Under these criteria, two participants were excluded from the analyses for excessive data loss (less than 50% usable trials in at least one condition). All the included participants had above 74% of usable data. We used R (RStudio, v1.0.153) and lme4 (Bates et al., 2015) to perform the analyses of the relationship between response time and pupil size. Response times were positively skewed. A common approach to correct for deviations of normality is to inverse transform response times (1/RT), however, applying nonlinear transformations can affect the interpretation of interactions. Thus, we used generalized linear mixed-effect Bayesian models assuming an inverse Gaussian distribution with inverse (-1/RT) link, which provide a solution to this problem by satisfying normality assumptions without the need for transformation (Lo & Andrews, 2015). Because pupil dilation and pupil baseline were partially correlated (r = .39), their effects were assessed in two separate models. Errors rates were analyzed through logistic regressions. *P*-values for each parameter estimate were calculated with likelihood ratio tests of the full model against the model without the effect in question. Bayesian models were created in Stan (http://mc-stan.org/) and brms package (Bürkner, 2017). Python and R scripts for data preprocessing and statistical analysis, and raw data are available in supplementary materials.

Results

Perceptual Load and Classic Interference

The attentional task utilized in this study was adapted from a commonly used visual search task for the study of perceptual load effects (Lavie, 1995, 2005; Theeuwes et al., 2004). In this task stimuli are usually displayed without controlling for luminance. However, because pupil size reflects both LC-NE activity and the light reflex, we adapted this task so that the stimuli were isoluminant with the background. Isoluminance may reduce contrast between the stimuli and the background and therefore we first assessed whether the classic effect of perceptual load were maintained under our manipulation.

	Compatible	Incompatible	I - C
Low Load	701 (1.5)	728 (2.9)	27*
High Load	1007 (14.3)	1002 (14.8)	-5

Table 1

Response times for the different load and compatibility conditions. There was a significant interaction between load and distractor compatibility, indicating that our manipulation successfully reproduced the effect of perceptual load on irrelevant distractor processing. Error rates (in percentage) are presented for each condition. * p < *.001.*

We hypothesized that perceptual load should modulate interference caused by a peripheral distractor (Lavie & Cox, 1997). In this, we expected an interaction between perceptual load and compatibility of distractor, where incompatible distractors should delay response times when they are processed (i.e., under low load where individuals still have available perceptual resources). In contrast, little or no distractor interference is expected in high perceptual load, where there is little spare capacity to process the peripheral distractor.

In order to analyze the results, we conducted a generalized Bayesian linear mixed-model analysis of response time. The model included load (high/low) and compatibility (compatible/incompatible) as main effects, random intercepts for participants, and random slopes for load and compatibility.

The results showed that, as expected, low load displays yielded significantly faster RTs than did the high load (1005 vs. 715 ms; $L = 22.52$, $df = 1$, $p < .001$). The effect of compatibility of the distractor had no significant main effect (853 vs. 840 ms; $L = 2.28$, $df = 1$, $p = 0.131$). However, in line with the perceptual load theory, there was a significant interaction between load (high vs. low) and type of distractor (compatible vs. incompatible). In high load the compatibility effect was only -5 ms, while in low load it was 27 ms, indicating an interaction estimate of 33 ms (95% CI [6; 61], $L = 7.763$, $df = 1$, $p = 0.005$). In the case of low load, the effect of incompatible distractors is to prolong response times by 27 ms (95% CI [15; 38], $L = 18.132$, $df = 1$, $p < 0.001$). In contrast, the compatibility effect in high load was not significant (L = 0.25, df = 1, p = 0.986). Total error rates were relatively low (9 %). There were less errors in the low load than in the high condition (L = 28.20, df = 1, p < .001). Compatibility did not affect error rates (L = 1.38, df = 1, p = .236) and there was no interaction between load and compatibility (L = 3.19, df = 1, p = .068). Overall, these results indicate that we were successful in designing isoluminant high- and low-load conditions that resulted in compatibility effects in the low-load condition and a no compatibility effect in the high-load condition.

Pupil Baseline vs. Perceptual Load

Pupil baseline fluctuations (see Figures 2 and 6) have been shown to be an indicator of LC-NE tonic activity (Joshi et al., 2016). LC-NE can have periods of higher or lower basal activity, which have been associated with shifts in attentional performance (Aston-Jones, 2005). In particular, low tonic LC activity was linked with better performance in attentional tasks (Aston-Jones & Cohen, 2005; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010). Therefore, if the pupil baseline preceding each trial reflects activity in the LC, we hypothesized that it should have a significant effect on search efficiency.

In order to compare the effect of baseline, the baselines preceding each trial were normalized by a resting state pupil size recorded after the calibration procedure of the eyetracker (see figure 2). As observed in Figure 3, the baseline preceding trial onsets were smaller in both the low (0.885, 95% CI [.945; .824]) and high (0.862, 95% CI [.916; .807]) perceptual load conditions compared to a resting state baseline. However a comparison between load conditions showed that their baselines did not differ significantly between each other (L = 0.703, df = 1, p = 0.402). A transition towards a smaller pupil size suggests a decrease in LC tonic activity, usually associated with improved attentional performance. In the case of our study, this shift suggest some attentional predisposition of the participants towards the upcoming task.

Baseline as Predictor of Response Time

We then investigated whether fluctuations in pupil baseline would predict search efficiency (as reflected by response times). For this purpose, we conducted linear mixed-effect analyses that included normalized trial baseline, perceptual load, and distractor compatibility as fixed effects. The model also controlled for trial order effects and included random intercepts for participants and random slopes for load.

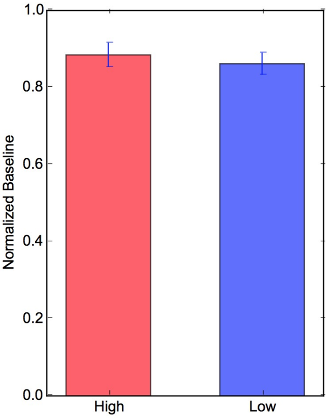

Figure 3. The pupil baseline prior the onset of each trial was normalized by a resting state baseline recorded during passive fixation. Trial baselines preceding each trial were on average smaller compared to a resting state baseline. However, there were no differences between conditions. Such decrease in pupil size seems to reveal attentional predispositions towards the upcoming attentional task. Error bars represent s.e.m.

The results indicated that the effect of the interaction between perceptual load and distractor compatibility, now controlling for pupil baseline, was found to remain significant compared to when no pupil size information was included (b = 55, 95% CI [17; 93], L = 7.92, df = 1, p = .004). In fact, a comparison between models showed that adding pupil baseline information significantly improved the model's fit (L = 26.49, df = 2, p < .001).

As observed in Figure 4, there was a significant interaction between load and pupil baseline in explaining search efficiency (b = 207, 95% CI [81; 333], L = 10.35, df = 1, p = .001). This interaction revealed an enhanced effect of baseline in conditions of low perceptual load. In particular, response times increased by 228 ms (95% CI [170, 288], L = 29.78, df = 1, p < .001)

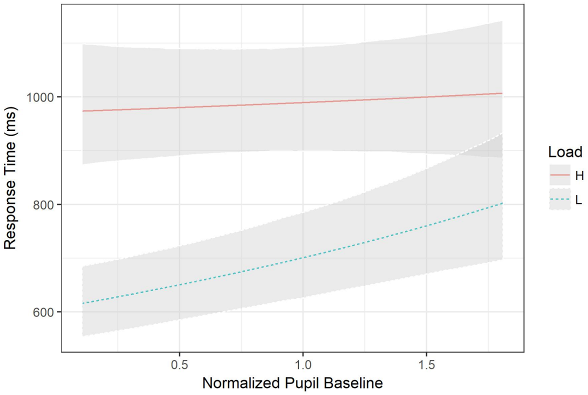

Figure 4. The effect of baseline pupil size on response time for high (H) and low (L) perceptual load. There was a significant relationship between pupil baseline and response time in conditions of low perceptual load. However, this relationship was not observed in high load. This differences suggest the involvement of distinct attentional mechanisms, where the role of pupil baseline seem to only influence one of such mechanisms. The plot displays fitted values and 95% credible intervals obtained from a Bayesian mixed model.

for every unit increase in pupil baseline (the smaller the baseline, the faster the participant's RTs). The effect of baseline going from a minimum to a maximum size is to slow down RTs by 183 ms (95% CI [103; 290] ms). Interestingly, the baseline did not predict search efficiency in high load (b = 20, 95% CI [-48, 88], L = 0.164, df = 1, p = 0.685). The interaction between baseline and compatibility was not reliable (b = -76, 95% CI[-175, 23], L = 2.31, df = 1, p = .128).

In addition to slowing down responses, pupil baseline did not significantly increase the log odds of commiting and error in low load (b = 1.6, 95% CI [3.79, -0.48], L = 2.16, df = 1, p = .141) or high load (b = 0.23, 95% CI [1.07, -0.61], L = .28, df = 1, p = .594). This indicated that the shift in response times cannot be attributed to speed/accuracy trade-offs.

Task-Evoked Pupil Dilation

Task-evoked pupil responses arise as a result of perceptual load processing. Pupil responses have been associated with load on working memory and mental effort (Kahneman & Beatty, 1966). As depicted in Figures 5 and 6, high perceptual load caused significantly larger peak pupil dilations than low load (16 vs 22%, L = 102.58, df = 1 p < .001).

The analyses showed that there was a significant effect of response time on pupil dilation, where larger pupil dilations correlated with slower response times (b = 302, 95% CI [196; 409], L = 57.79, df = 1, p < .001), which can be observed in Figure 7. As for the baseline, there was a significant interaction between pupil dilation and perceptual load, where the role of pupil dilation was significantly enhanced in predicting response times in high perceptual load (b = -199, 95% CI [-318; -191], L = 8.21, df = 1, p = .004). In particular, the effect of response time on pupil dilation was significant in low perceptual load (b = 148, 95% CI [55; 241], L = 9.65, df = 1, p = .002) and high load (b = 340, 95% CI [245, 435], L = 45.40, df = 1, p < .001). There were no differences in the amplitude of pupil dilation as function of distractor compatibility (b = 78, 95% CI [-44; 201], L = 1.58, df = 1, p = .209).

Larger pupil dilations were associated with an increase of 3.97 in the log odds of making an error (L = 36.11, df = 1, p < .001), an effect that was more pronounced in low load (log odds = 4.90, 95% CI [8.29, 1.56], L = 7.77, df = 1, p = .005).

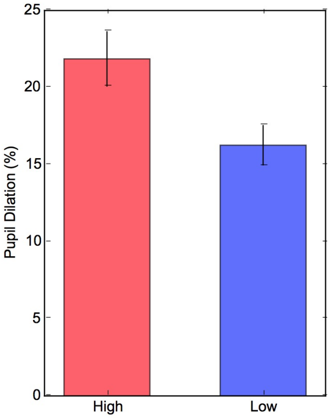

Figure 5. The figure shows pupil dilation relative to baseline for low and high perceptual load. The amplitude of pupil dilation was larger in high load ($p < .001$). Error bars denote s.e.m.

Pupil Peak Dilation Timing

The timing to peak dilation followed a dynamic similar to that observed for pupil dilation amplitudes reported in the previous section. There was a main effect of peak dilation time in predicting response times (b = 125, 95% CI[108, 143], L = 191.78, df = 1, $p < .001$). There was also a significant interaction with load (b = -153, 95% CI [-173, -135], L = 72.93, df = 1, $p < .001$). In particular, the relationship between peak time and response time was less pronounced in low load (b = 60, 95% CI [40, 80], L = 32.51, df = 1, $p < .001$), than in high load (b = 216, 95% CI [189, 243], L = 184.87, df = 1, $p < .001$).

Discussion

This study is the first to relate LC-NE function, as measured through pupil size, with search efficiency in conditions of high and low perceptual load. According to recent evidence, fluctuations in pupil size serve as a proxy of LC-NE activity (Joshi et al., 2016), which, in turn, is associated with cognitive and attentional mediation (Aston-Jones & Cohen, 2005). The analyses presented here show that the pupil baseline preceding each trial exclusively predicted the upcoming search performance in conditions of low perceptual load (see Figure 4). In low load, all stimuli are believed to receive full perceptual processing, leading selection to occur at a late processing stage. In contrast, this relationship between pupil baseline and response time was no longer significant in high load, which relies on early selection mechanism (Lavie & Cox, 1997). Furthermore, the results could not be explained in terms of eye-movements or trial order effects. In line with the perceptual-load theory (Lavie, 1995) and dilution accounts (Chen & Cave, 2013; Tsal & Benoni, 2010), the results show that the extent to which LC-NE activity influenced search efficiency was determined by the perceptual load of the task at hand.

LC activity is believed to modulate arousal and cortical functions (Aston-Jones & Cohen, 2005; Sara & Bouret, 2012a), with extensive influence over behavioral states (Aston-Jones & Cohen, 2005). The present analysis of pupil baseline shows that there was a significant decrease in pupil size as participants engaged in the experimental tasks (Figure 3) compared to when pupil size was measured during passive fixation (Figure 2). This may correspond with evidence showing that low tonic LC-NE activity (also revealed by small pupil size) correlates with periods of good attentional performance in go/no-go tasks (Gilzenrat et al., 2010; Usher, 1999) and improved neural representations of sensory inputs (Warren et al., 2016). Thus, this shift in pupil baseline seems to reveal some attentional preparatory mechanisms in anticipation for perceptual processing.

The LC presents spontaneous fluctuations in tonic level that translate into changes in pupil size, as observed during passive fixation (see Figures 2 and 6). Here, we show that this variability in baseline size across trials predicted search performance, specifically in conditions of low perceptual load. In the context of a visual search task, low perceptual load allows participants to perform an efficient (i.e., ‘pop-out’) search for the target (Lavie & Cox, 1997), where all stimuli receive perceptual resources and selection occurs late in processing. In contrast to early mechanisms, late selection relies largely on control functions, as evidenced by poorer attentional performance when working memory is taxed (De Fockert, 2013; Lavie, 2010). Thus, we interpret our results as suggesting an interaction between LC-NE action and selection mechanisms: in low

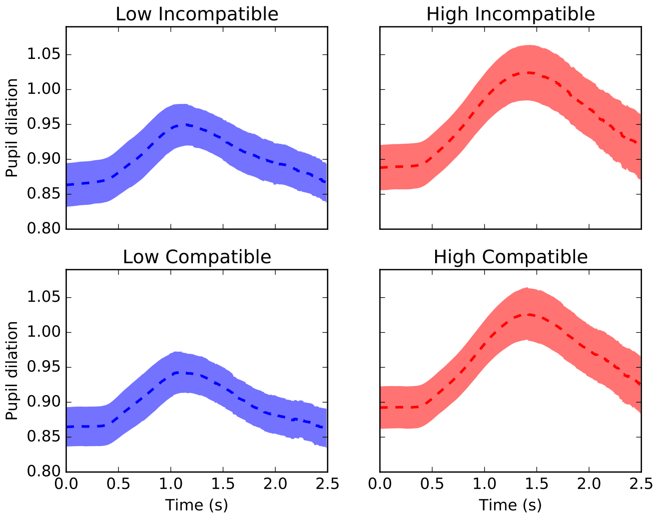

Figure 6. Pupil responses for each condition. For visualization purposes, pupil responses are shown relative to resting baseline size. Pupil responses are time-locked to the moment of stimulus onset (0 s). As observed in the figure, pupil baselines prior trial onset were on average smaller than during passive fixation. Shaded areas represent s.e.m. at each time point.

load, selection depend on late mechanisms, which, in turn might as well be modulated by LC-NE activity. In contrast, LC-NE would not influence search efficiency in high perceptual load performance because early selection mechanisms rely on perceptual capacity limitations.

Recently, the perceptual load model was rivaled by an alternative account suggesting that the reduction in distractor interference under high perceptual load is due to “dilution” of the distractor within the irrelevant letters in the search array (Benoni & Tsal, 2013; Cave & Chen, 2016; Tsal & Benoni, 2010; Wilson, Muroi, & MacLeod, 2011). Although both models differ on the selection mechanisms in high load, both agree on the fact that distractors are more likely to be processed under low perceptual conditions, when selection relies on late mechanisms. Therefore, the results presented here fit with predictions derived from both the perceptual load and dilution accounts.

As described above, pupil baseline predicted search efficiency (as reflected by faster response times), however, it did not predict response errors. First, this is indicative that the improvement in response times cannot be attributed to speed/accuracy trade-off mechanisms. Secondly, this contrasts with experiments in monkeys using a go/no-go task reporting that high tonic LC activity were associated with increased false positives (Aston-Jones et al., 1994; Gilzenrat et al., 2010; Usher, 1999). This difference may rely in the fact that “go” responses in such tasks had to be performed within strict time constraints, forcing speeded responses. In addition, the present task tests divided attention across stimuli within the search display, rather than the monitoring of a rapid visual stimuli presentation as in these studies.

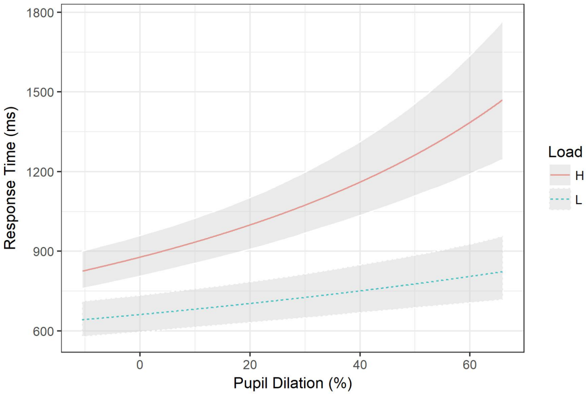

Figure 7. Pupil dilation and response times for high (H) and low (L) load. There was a positive relationship between pupil dilation and response times in both conditions. However, this relationship was enhanced in conditions of high perceptual load. The plot displays fitted values and 95% credible intervals obtained from a Bayesian mixed model.

Pupil Dilation

The processing of the search arrays was followed by a phasic increase in pupil size. The results showed an interaction between search efficiency and pupil responses. In this case, both the timing and the amplitude of pupil dilation were significant predictors of response times in both low and high perceptual load. This interaction indicates that the effect of pupil dilation was significantly more pronounced in conditions of high load, when the system was perceptually overloaded (see Figure 7).

Pupil dilation has received more attention in psychological research than pupil baseline. For instance, pupil dilation has been long associated with memory load and mental effort (Kahneman & Beatty, 1966). In particular, several articles reported that pupil dilation reflects the time course of decision making during perceptually challenging tasks involving both visual (de Gee et al., 2014; Einhäuser et al., 2008) and emotional stimuli (Oliva & Anikin, under review). The results of this study are in line with these previous report, adding that this relationship may be stronger depending on the perceptual demands of the task.

Pupil dilation has been shown to provide short latency information of up to 100 ms despite its slow latency dynamics (Zylberberg, Oliva, & Sigman, 2012). However, the resolution of pupil responses did not allow us to distinguish between compatible and incompatible trials, with temporal differences between conditions largely below such value.

All in all, the results of the present study reveal an interaction between pupil baseline and attentional performance as a function of perceptual load that is in line with the perceptual-load hypothesis and with current views of LC-NE function (Aston-Jones & Cohen, 2005). The results show that the degree with which LC-NE influences behavioral performance is related to the perceptual load of the task at hand. Thus, this study link early and late selection mechanisms as defined by the perceptual-load hypothesis with LC-NE function, as measured by pupil size.

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