to date for the feasibility of sympatric speciation driven by social selection. □

Methods

Mitochondrial DNA analyses. A 4-kb portion of the mtDNA (including the A + T-rich noncoding region) was amplified by polymerase chain reaction (PCR) from a single queen per nest and digested with the restriction enzymes *Bam*HI, *Dpn*II, *Eco*RV, *Eco*RI, *Hae*III, *Hha*I, *Hin*dIII, *Hin*fI, *Kpn*I, *Msp*I, *Rsa*I, *Taq* I and *Xba*I (K.G.R. and D.D.S., manuscript submitted). Digestion products were separated electrophoretically in 1.5% agarose gels, stained with ethidium bromide, and visualized using ultraviolet light. To confirm that the desired region of the mtDNA molecule was amplified, one end of the PCR product was sequenced and aligned with a previously published sequence from the honey bee[27]. Maternal inheritance of the 4-kb fragment was demonstrated by examining the variable digestion products from the enzyme *Taq*I in nestmates from ten monogyne colonies. The presence or absence of restriction sites inferred using complete and partial digestion procedures defined the composite haplotypes.

Estimation of *Pgm-3*^{b} and *Gp-9*^{b} frequencies. The genotypes of M queens and their single mates were inferred by inspecting genotype arrays for female and male offspring from single M nests. Such reconstruction of parental genotypes is possible because a queen's sons arise from her unfertilized eggs and her daughters arise from eggs fertilized by the sperm of a single haploid male[24,28]. For P queens and wild-caught males, allele frequencies were estimated using a resampling procedure when more than one individual was collected per nest[15]. Wild-caught males from P nests were confirmed to be fertile haploids on the basis of their size and their banding patterns at four allozyme loci[13]. Methods for scoring genotypes at *Pgm-3* and *Gp-9* and evidence for Mendelian inheritance of the products of these genes are presented elsewhere (refs 13, 28 and K.G.R., manuscript submitted). Sample sizes for estimating *Pgm-3*^{b} and *Gp-9*^{b} frequencies are as follows. Eastville M site: *Pgm-3*^{b}, egg-laying queens and their male mates from 41 nests, 149 wild-caught males from 19 nests; *Gp-9*^{b}, egg-laying queens and their male mates from 67 nests. All M sites: *Pgm-3*^{b}, egg-laying queens and their male mates from 118 nests, 497 wild-caught males from 62 nests; *Gp-9*^{b}, egg-laying queens and their male mates from 149 nests. All P sites: *Pgm-3*^{b}, egg-laying queens from 427 nests, 140 wild-caught males from 28 nests; *Gp-9*^{b}, egg-laying queens from 427 nests.

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Word meanings can be accessed but not reported during the attentional blink

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After the detection of a target item in a rapid stream of visual stimuli, there is a period of 400–600 ms during which subsequent targets are missed. This impairment has been labelled the 'attentional blink'[1]. It has been suggested that, unlike an eye blink, the attentional blink does not reflect a suppression of perceptual processing, but instead reflects a loss of information at a postperceptual stage, such as visual short-term memory[2–4]. Here we provide electrophysiological evidence that words presented during the attentional blink period are analysed to the point of meaning extraction, even though these extracted meanings cannot be reported 1–2 s later. This shows that the attentional blink does indeed reflect a loss of information at a postperceptual stage of processing, and provides a demonstration of the modularity of human brain function.

To test whether the attentional blink reflects a postperceptual impairment in processing, we recorded event-related potentials (ERPs) from normal young adults and measured the 'N400' peak, (a negative peak at 400 ms poststimulus) which reflects the degree of mismatch between a word and a previously established semantic context[5–7]. For example, a large N400 would be elicited by the last word of the sentence 'The man wore blue trousers and a green bucket', but not by the last word of the sentence 'The man wore blue trousers and a green shirt'. Because a word must be identified before it can be compared with a semantic context, the presence of an N400 peak for a mismatching word indicates that this word has been identified. Thus the presence of a normal N400 in our study would provide strong evidence that words presented during the attentional blink are fully identified, even though subjects cannot accurately report them.

As shown in Fig. 1, each trial in this experiment began with the presentation of a 'context word' that created the semantic context for that trial. A stream of 20 seven-character strings of letters or numbers was then presented at a rapid rate of one string every 83 ms. Most were distractor items consisting of randomly selected consonants, drawn in blue. Either the seventh or the tenth string served as the first target on a given trial, and this string consisted of a randomly selected digit, repeated seven times (to create a seven-character string). The second target consisted of a word of 3–7 characters, drawn in red. We will refer to this second target as the 'probe' word. At the end of the trial, a question mark appeared, signalling the subject to make two button-press responses. These responses indicated whether the first target was an odd digit or an even digit and whether the probe word was semantically related or unrelated to the context word for that trial. The context word and probe word were either closely related (for example, jam and jelly) or clearly unrelated (for example, shoe and mouse). A control condition was also included in which subjects ignored the first target.

The probe word was always the first, third or seventh string after the first target (denoted below as lag 1, lag 3 and lag 7). Previous studies have shown that the attentional blink is typically strongest at lags 2–3 and usually ends by lags 6–8, with little or no impairment in accuracy at lag 1 (refs 1–3). As shown in Fig. 2*a*, we found the same pattern of results. Specifically, accuracy for the

probe word was 87–90% correct at lags 1 and 7, but dropped to 66% correct at lag 3. Accuracy for identifying the relatedness of the probe word was higher at all lags in the control condition than in the experimental condition and showed no decline at lag 3, resulting in giving a statistically significant main effect of condition ($P < 0.001$) and a significant interaction between lag and condition ($P < 0.001$).

Our main question was whether the probe-elicited N400 peak, like probe discrimination accuracy, would also be reduced at lag 3 in the experimental condition. The analysis of the N400 was complicated by the high stimulation rate, which caused the ERP elicited by the probe word to be overlapped by the ERPs elicited by the previous and subsequent stimuli. To avoid this problem, we constructed 'difference waves' in which the ERPs elicited by probe words that were related to the initial context word were subtracted from the ERPs elicited by unrelated probe words. Because these two trial types were identical except for the relationship between the probe word and the context word, only the potentials that were influenced by this relationship (the N400) remained in the difference wave.

As shown in Fig. 3, the difference waves consisted primarily of a negative-going potential that had the typical characteristics of the N400 component[5,8]: it peaked at roughly 400 ms, was largest at the central and parietal midline electrodes, and was slightly larger over the right hemisphere than the left. The N400 was significantly smaller in the experimental condition than in the control condition ($P = 0.01$), which reflects the lower overall accuracy in this condition and demonstrates the sensitivity of the N400. As shown in Fig. 2*b*, however, there was no significant effect of lag on N400 amplitude in either the experimental condition or the control condition, despite the large drop in accuracy at lag 3 in the experimental condition ($P > 0.35$ for both the lag main effect and the lag × condition interaction).

Thus, although the N400 seems to be a sensitive index of semantic-mismatch detection, the attentional blink was not accompanied by a reduction in the N400 elicited by a semantic mismatch. This is especially remarkable given that we observed a substantial decrease in the ability of our subjects to report this semantic mismatch at the end of the trial, 1–2 s after the peak of the N400. This dissociation between N400 amplitude and discrimination accuracy implies that many of the errors at lag 3 in the experimental condition occurred despite correct semantic analysis, which should in turn have led to the presence of an N400 on these error trials. This prediction was tested in a separate analysis of the ERPs elicited on trials with incorrect responses for the probe word. In the experimental condition, the N400 on these error trials was found to be significantly larger at lag 3 than at lags 1 or 7 ($P < 0.05$). Together with the lack of a suppression at lag 3 on correct trials, these results provide strong evidence that the decline in probe discrimination accuracy during the attentional blink was not caused by a suppression in perceptual processing, but was instead a result of a postperceptual loss of information.

Our findings have implications beyond the simple question of whether the attentional blink operates at an early or late stage. First, the finding of no perceptual suppression during the attentional blink period contrasts with the results of spatial-attention experiments, in which the N400 peak and the sensory-evoked P1 and N1 peaks (the initial positive and negative ERP peaks) are suppressed for stimuli presented at ignored locations compared with attended locations[9–12]. This suggests that the attentional mechanisms that underlie the selection of perceptual information from a spatial array are different from the mechanisms that underlie the selection of more highly processed conceptual information over a period of time. This independence of perceptual and postperceptual processes may be important for tasks that involve selection at both low and high levels, such as reading, because it may allow the faster low-level perceptual processes to operate asynchronously from the slower high-level processes[13]. These findings also contribute to our understanding of the general architecture of the human cognitive system, by indicating that the meaning of a word can be extracted and compared with other semantic information without reaching a stage at which the results of this comparison can be retained for even 1–2 s. This may further indicate that substantial semantic processing can occur in the absence of awareness, although it is difficult to determine whether the probe words were identified without reaching awareness or if they momentarily reached awareness and were then rapidly forgotten. □

Stimulus Type	Time (ms)	Related Trial	Unrelated Trial
Context Word	1000	RAZOR	WHEEL
Blank	1000		
Distractor	83	PNVCSZP	KDSWPVZ
Distractor	83	GRSDPKN	VNMCPKL
Distractor	83	BVCPLMS	FDPMCNV
Distractor	83	DSPWTFR	VPMTDZM
Distractor	83	RLDJHGK	HJDLGFP
Distractor	83	SPLDJMF	DFPLJKH
First Target	83	3333333	4444444
Distractor	83	WDPTBNF	GHJDMVT
Distractor	83	SCDPVBF	HDVCBNM
Probe	83	XSHAVEX	XJEWELX
Distractor	83	FDLNLKB	NMCVPHJ
Distractor	83	DLJJCNW	DCVPBJM
Distractor	83	WPSCDSN	PCNBVLK
Distractor	83	DPWVCPB	NPMTVDK
Distractor	83	CBNDPNJ	BRTFPMF
Distractor	83	RTPMVBC	JLSDCDK
Distractor	83	TWSCLMN	LKSDVCP
Distractor	83	LJVBCMH	DKKHNVP
Distractor	83	RMVCPKL	WKLDMZP
Distractor	83	DPNMNVZ	CPNHVGB
Blank	1000		
Response Cue	2000	?	?
Blank	2000		

FIG. 1 Example stimulus sequences for trials on which the probe word was either related or unrelated to the context word. The probe word was presented in red and all other items were drawn in blue. Also note that the probe word was flanked by Xs, when necessary, to create a total of seven characters in the string.

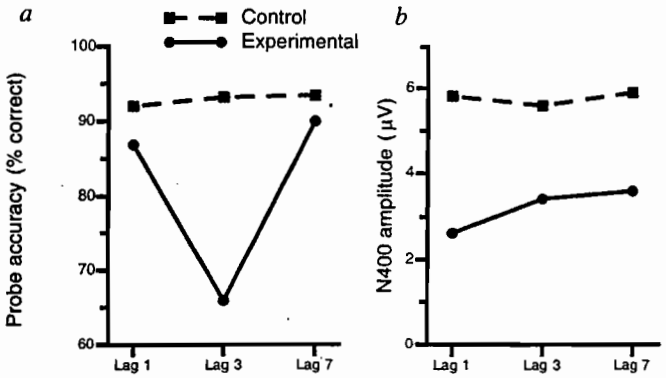

FIG. 2 *a*, Probe-discrimination accuracy as a function of lag (lag of 1-, 3- or 7-strings) for the experimental and control conditions. These values reflect only the trials on which the first target was correctly discriminated (first-target accuracy was 96% correct overall, with no effect of lag). *b*, Mean N400 amplitude as a function of lag for probe words in the experimental and control conditions, measured from the unrelated – related difference waves and averaged across electrode sites. N400 amplitude was computed as the mean amplitude of electrical activity between 300 and 500 ms poststimulus, relative to a 200-ms prestimulus baseline, at the F3, Fz, F4, C3, Cz, C4, P3, Pz and P4 electrode sites.

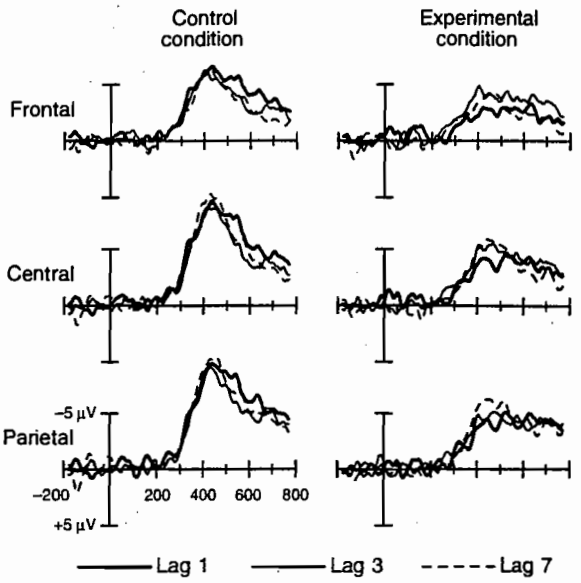

FIG. 3 ERP difference waves at frontal, central and parietal electrode sites along the midline (Fz, Cz and Pz), averaged across the 14 subjects. These waveforms were produced from averages that included only the trials on which the first target was correctly discriminated, but were not sorted according to the accuracy of the response to the probe word. The waveforms were low-pass filtered by convolving them with a gaussian impulse-response function with a standard deviation of 10 ms and a 50% amplitude cutoff of 20 Hz. Time zero represents the onset of the probe word. Note that, by convention, negative is plotted upwards.

Methods

Each string subtended 4.9° × 0.8° of visual angle. The first target was equally likely to be an odd or even digit, and the probe word was equally likely to be related or unrelated to the context word. Each subject received six 60-trial blocks in the experimental condition (in which both targets required a response) and six 60-trial blocks in the control condition (in which only the probe word required a response) in counterbalanced order. ERPs were recorded from 14 right-handed, neurologically normal native English speakers using our standard recording procedures[11] and electrodes located at 15 standard electrode sites (International 10/20 system) spanning the scalp. Analysis of variance was used for all statistical tests.

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Role of posterior parietal cortex in the recalibration of visually guided reaching

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VISUALLY guided reaching requires complex neural transformations to link visual and proprioceptive inputs with appropriate motor outputs[1,2]. Despite the complexity of these transformations, hand–eye coordination in humans is remarkably flexible, as demonstrated by the ease with which reaching can be adapted to distortions in visual feedback. If subjects attempt to reach to visual targets while wearing displacing prisms, they initially misreach in the direction of visual displacement. Given feedback about their reaching errors, however, they quickly adapt to the visual distortion. This is shown by the gradual resumption of accurate reaching while the prisms remain in place, and by the immediate onset of reaching errors in the opposite direction after the prisms have been removed[3]. Despite an abundance of psychophysical data on adaptation to prisms, the functional localization of this form of sensorimotor adaptation is uncertain. Here we use positron emission tomography (PET) to localize changes in regional cerebral blood flow (rCBF) in subjects who performed a prism-adaptation task as well as a task that controlled for the sensory, motor and cognitive conditions of the adaptation experi-

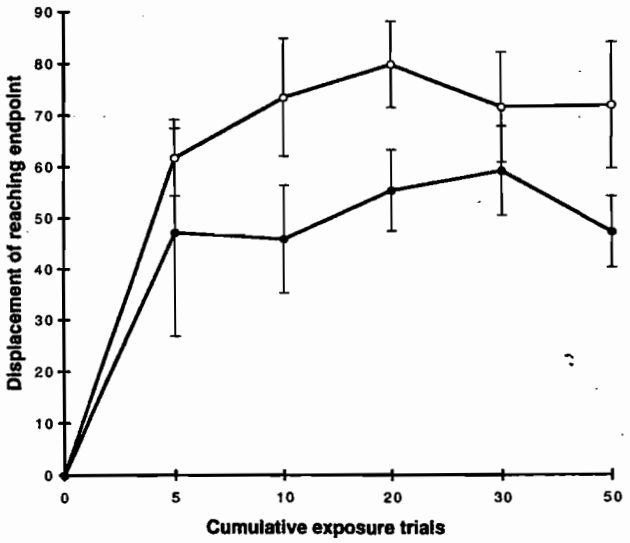

FIG. 1 Time course of prism adaptation as measured by after-effects both in visually targeted reaching and in the perception of hand position. Six subjects were tested separately on an adaptation task where after-effects were measured after 5, 10, 20 and 50 cumulative exposure trials with a rightward displacing prism (group means ± s.e.m.). Reaching after-effects (open circles) were measured as subjects reached to the remembered location of a visual target with prisms removed. We also measured proprioceptive after-effects (filled circles) as subjects attempted to reach reach with eyes closed to a point in front of the nose. Both types of after-effects (measured as differences between pre- and post-exposure reaching end points) were maximized after 5–10 exposure trials and did not increase further during longer exposures. Units on the ordinate represent screen coordinates along the horizontal axis (the axis of prismatic displacement).